Spawning and Development of Some Hawaiian Marine Gastropods[1]

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MANY PERSONS, at various marine biological stations situated throughout the world, have investigated the spawning habits and larval development of marine gastropods. Some of the recorded observations date back to the middle part of the last century or earlier. Various methods have been employed to obtain the materials for study, but always the effort put forth has been well rewarded, for the field is exceedingly rich. It is noteworthy that the study of plankton alone has been able to throw much light on the metamorphosis of the larvae of many species. This is a field of investigation that has an economic as well as an academic value, inasmuch as these minute planktonic larvae make a considerable contribution to the food supply of larger organisms, which in turn may serve as food for fishes that are of direct economic importance to man.

The investigations recorded here are the first to be published from this area of the Pacific. All the studies were done at the Marine Biological Laboratory of the University of Hawaii during the years 1920–1925, since which time nothing has been added. There are several reasons for this delay, the main one being the difficulty of publication. This required, among other things, much painstaking labor by a skilled person to adapt the many illustrations for reproduction.

Many illustrations were required to clarify the text and to enable the reader to compare the corresponding stages of species of the same genus. All the figures were drawn in lead pencil by the author from observation under low power of the compound microscope. A micrometer scale was used so that measurements in fractions of millimeters could be made readily.

All the species investigated were obtained in water not over 3 meters in depth, and most of the egg structures were deposited in the laboratory by isolated animals. When the spawns were obtained from the reefs, or elsewhere, careful checks had been made to ascertain their identity, which in most cases was later verified. No record of any species whose generic position was unknown has been included. Hence, discussion of a considerable number of additional species of the Nudibranchiata, whose systematic position has not yet been fully determined, awaits later publication.

No histological sections of embryos and larvae were made, all notes being from external observations. It will be noted that the ova of the various groups of gastropod mollusks discussed here were of the telolecithal type with holoblastic cleavage, of which the first two divisions were almost always equal, while the third division resulted in some blastomeres of minute size and with a small amount of yolk and other larger ones with much yolk. A trochophore stage of very short duration has been observed in some species, while a long veliger stage seems to be present in all. In no case has a metamorphosis from the veliger larva to the adult form been observed, nor even started, although a record was obtained of 21 days of free-swimming existence.

Included in this publication are the results of the study of the development of 41 species which are placed in 28 genera belonging to

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25 families of 3 orders. A key is furnished to aid in the identification of the spawn.

Material collected and in the author's possession consists of egg structures preserved in formaldehyde and balsam mounts of cleavage stages and veliger shells on slides.

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KEY TO THE SPAWN OF SOME HAWAIIAN MARINE GASTROPODS

1. Egg structure consisting of distinct, attached capsules with parchment-like walls or a continuing filament 2
   Egg structure otherwise, more or less aberrant 23

2 (1) Egg structure capsular with compact parchment-like walls 3
   Egg structure consisting of a continuing filament 5

3 (2) Capsules small, 1.5–4 mm. in length, pale yellow 4
   Capsules large, 8 x 10 mm. to 13 x 15 mm., squarish, flat and baggy, more or less corrugated marginally; attached to rock at basal margin or to one another (*Conus omaria,* p. 90); with elongate slit at distal margin which is closed during incubation. Color pale yellow or pink. . . **Conus,** p. 89

4 (3) Capsules oblong, rounded or pointed; adhering to one another in compact masses. Egg mass covered by foot of animal during incubation. Color pale yellow. . . **Cypraea,** p. 78.
   Capsules elongate, pointed; attached to substratum . . . . . **Mitra,** p. 86.

5 (2) Egg structure a cylindrical filament 6
   Egg structure a ribbon or band . 15

6 (5) Filament long, thin and tangled 7
   Filament short, thick and not tangled 10

7 (6) Filament from 0.5 mm. to 1 mm. in diameter 8
   Filament about 0.25 mm. in diameter, thread-like, comprising many separate threads forming a bundle spread over 4 square cm. Color pale yellow. **Strombus maculatus,** p. 95.

8 (7) Filament of great length, about 1 mm. in diameter, adhering in a compact mass, attached to underside of rocks and spread over an area of 25 square cm. Color pale yellow when freshly laid, brown when embryos are near hatching. . . . . **Tethys grandis** and **T. bipes,** pp. 98, 99.
   Filament not of great length, occupying an area from 2 to 4 square cm. Color pale yellow. 9

9 (8) Filament compactly tangled and attached to substratum . . . . . **Clava obeliscus,** p. 95.
   Filament loosely looped or tangled and festooned on algae . **Tethys elongata,** p. 100, and **Notarchus striatus,** p. 101.

10 (6) Filament with ova transversely arranged in loops within, and visible to the unaided eye . . 11
   Filament without transversely arranged ova 12

11 (10) Filament large, forming an elliptical loop. Length 18 cm., diameter 4 mm. Color white. . . . **Pleurobranchus** sp., p. 107.
Filament small, forming a circular loop. Length 3 cm., diameter 1 mm. . **Bulla** sp., p. 103

12 (10) Filament slender and tapering to an acute point at the extremities 13
Filament thick with obtuse or blunt extremities with or without spiral twists 14

13 (12) Filament forming one volution without loops. Length 19 mm., diameter 1 mm. Color white. . . . . **Placobranchus** sp., p. 107.
Filament with a few irregular loops. Length 25 mm., diameter 0.5 mm. Color white. . . . . **Elysia** sp., p. 108.

14 (12) Filament with one or two turns, flatly arranged. Length from 2.5 to 4 cm. Color white. . . . . **Morula dumosa,** p. 96, and **Haminoea crocata,** p. 104
Filament with three and a half spiral turns, with one end attached to a gelatinous base or to the substratum. Length 35 mm., diameter 3 mm. Color white. . . . . **Bullina scabra solida,** p. 103.

15 (5) Ribbon attached by one edge or by a basal support to substratum 16
Ribbon attached flatly to substratum 22

16 (15) Ribbon a much-folded mass attached by a basal support to substratum about 2.5 cm. in height and 1.5 cm. in width. Color white. . . . . **Hydatina amplustre,** p. 102, and **H. physis,** p. 102.
Ribbon attached by one edge to substratum 17

17 (16) Ribbon very large and intensely folded, forming three or four circularly wound volutions which measure about 13 cm. across. Color pink. . . . . **Umbraculum sinicum,** p. 105.
Ribbon small and with only slight folds or none 18

18 (17) Ribbon rising vertically from margin of attachment 19
Ribbon sloping outward from centrally placed margin of attachment 21

19 (18) Ribbon of one volution; extremely small white band, about 4 mm. in length . . . . . **Glossodoris** sp., p. 109.
Ribbon of 2 to 3 volutions, 2 to 3 cm. across the mass 20

20 (19) Ribbon bright scarlet or deep orange, forming two volutions, about 14 cm. long and 6 mm. wide . . . . . **Hexabranchus** sp., p. 109.
Ribbon bright yellow, forming 3 volutions, about 11 cm. long and 4 mm. wide . . . . . **Cryptodoris** sp., p. 109.

21 (18) Ribbon with one volution. Diameter of entire structure about 1 cm. Color bright yellow. . . **Aeolidia** sp., p. 110.
Ribbon with several irregular volutions, 7 mm. wide. Color white. . . **Melibe pilosa,** p. 111.

22 (15) Ribbon with numerous parallel loops, not overlapping, 0.33 mm. wide. Clear and colorless. . . . . **Dolabrifera olivacea,** p. 100.
Ribbon not looped, forming a half circle, about 3 cm. long, 2 mm. wide. Colorless. . . . . **Siphonaria normalis amara,** p. 111.

23 (1) Egg structure consists of groups of unattached, minute capsules, each containing 1 or 2 ova. The capsules about 0.2 mm. in diameter. . . . . **Littorina pintado,** p. 97.

Egg structure not capsular . . . 24

24 (23) Egg structure a gelatinous mass 25

Egg structure not a gelatinous mass but orbicular or fan-shaped and of great size. Diameter 15 cm., thickness about 2 mm. Ova grouped together in masses of about 50, visible to the unaided eye and arranged in transverse rows of about 50. Color pale yellow. . . **Tonna perdix,** p. 96.

25 (24) Egg mass consisting of a globular, soft, clear gelatinous matrix about 18 mm. in diameter in which about a thousand purple-colored ova are imbedded. . . . . **Atys semistriata,** p. 105.

Egg mass of irregular outline, tough, gelatinous, and pasted flatly to any surface, occupying about 5 square cm. Color lemon yellow. . . . . **Peronia** sp., p. 112.

Order PROSOBRANCHIATA
Family *CYPRAEIDAE*

Genus CYPRAEA

Cypraea carneola Linnaeus

Figs. 1, 2

On June 8, 1921, a large adult specimen of *Cypraea carneola* was found on the Waikiki reef, off the Marine Biological Laboratory of the University of Hawaii. This species is not of common occurrence in wading depths on the Hawaiian reefs.

The specimen was brought to the laboratory and placed in a trough with running water, and the following night it deposited an egg mass on the enameled surface of a pan in which it was placed. The egg mass consisted of about 1,000 egg capsules which were imbedded in a firm gelatinous substance.

The individual egg capsule, or egg case, is about 4 mm. long and is triangular, with its flattened base attached to the substratum or to another egg capsule. From its base the egg capsule curves slightly to a somewhat obtuse point (Fig. 1*a*). Its firm parchment-like walls are pale yellow and contain, in a clear viscid capsular fluid, an average of 500 ova (Fig. 1*b*).

During the first day the animal remained constantly on its eggs, covering the entire mass with its foot; thereafter, probably due to having been removed several times, it left its "nest" voluntarily and stayed away.

Under the compound microscope the cleavage of the zygote was studied, as were the resulting embryos as far as the free-swimming larval stage.

The ovum is about 0.14 mm. in diameter, and a concentration of cytoplasm containing the nucleus appears as a clear area about one-fifth the diameter of the ovum. This in turn is surrounded by a dark area, while somewhat globular yolk granules constitute the bulk of the ovum (Fig. 1*c*).

Upon examination of the contents of one of the egg cases the morning after they were laid, none of the zygotes was found to have started cleavage. The contents of another egg case, however, opened at 4:00 P.M. of the same day, revealed many in the two-cell stage scattered among those which had not started cleavage.

This is a telolecithal egg with holoblastic, or total, cleavage, the first two divisions being equal, the third unequal. The first cleavage is vertical and passes through the animal and vegetal poles of the zygote, dividing it into two blastomeres of equal size. The animal, or formative, pole is clearly discernible by the position of the nuclei, the nucleus of each daughter cell being directly opposite that of the other, and close to the cleavage plane (Fig. 1*d*).

An hour later, at about 5:00 P.M., the second division began to take place; and in the

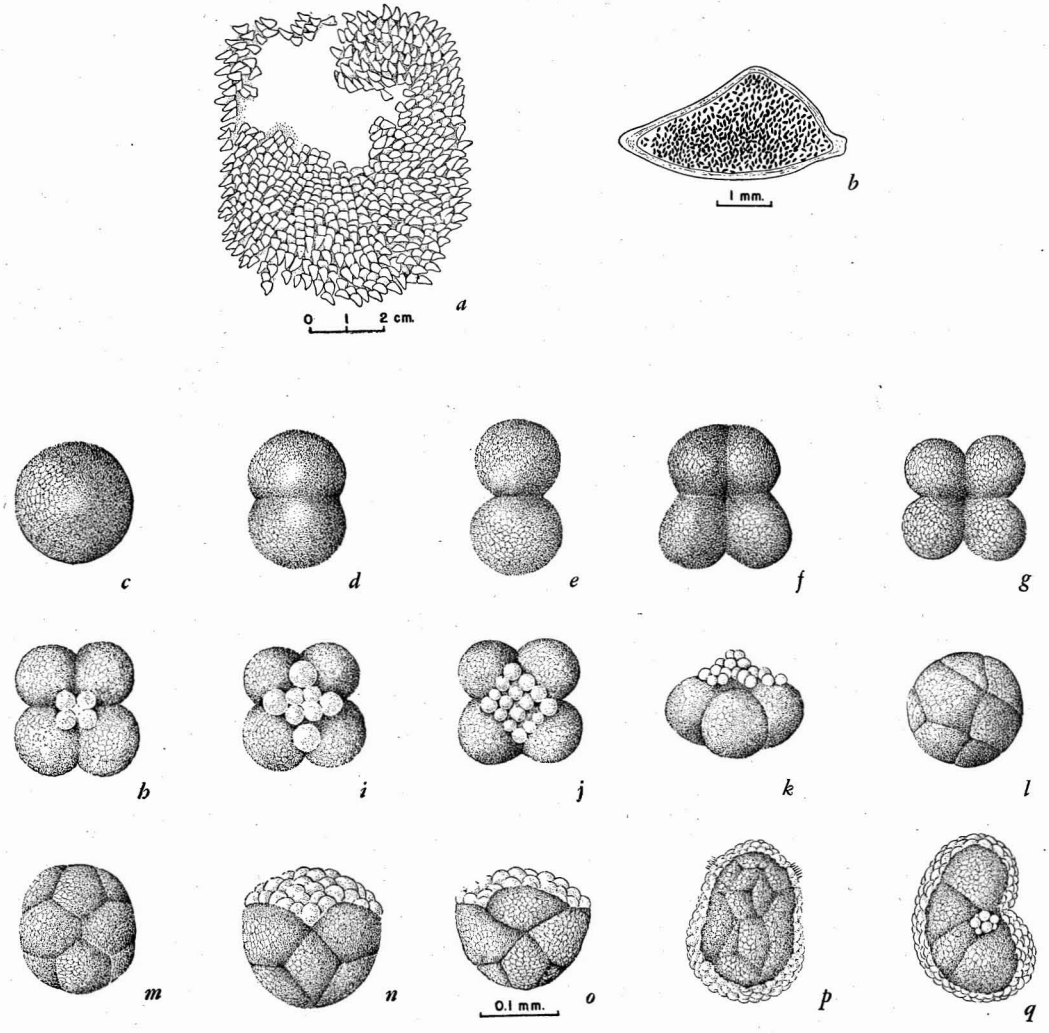

FIG. 1. *Cypraea carneola* Linnaeus. *a,* Egg mass; *b,* capsule enlarged; *c–n,* cleavage stages; *o,* blastula stage; *p,* trochophore stage; *q,* gastrula stage.

course of about ½ hour, nearly all the embryos in the two-cell stage had completely divided into four blastomeres of equal size, symmetrically arranged, and joined together by their inner surfaces. Like the first cleavage, this was vertical and at a right angle to the first. The nuclei of the blastomeres were grouped together about the animal pole. Following each of the preceding cleavages, a contraction and rounding off of the blastomeres occurred which resulted in their being joined at the cleavage planes by a comparatively small area (Fig. 1*g, h*).

By 11:00 P.M., another division had taken place in the horizontal plane and at right angle to the two preceding cleavages forming four micromeres and four macromeres (Fig. 1*h*).

At about the same time some embryos had undergone an additional division of the macromeres, thus producing four more micromeres, arranged outside of the others and located in the line of division between the macromeres. The cells of this division were

about twice the volume of the preceding (Fig. 1*i*).

By the following noon, July 10, the micromeres in many of the embryos had increased to 16 in number and, in some instances, they were arranged in orderly rows of four at the animal pole. These cells did not differ much in size; the larger ones were at the outer angles and were, on an average, a little smaller than the first four micromeres. This result had apparently come about through further divisions of the eight micromeres observed in the preceding stage (Fig. 1*j*).

At this time in some of the embryos an additional division of a number of the micromeres had resulted in a crowding together and a piling up into a pointed dome of these small cells at the animal pole (Fig. 1*k*).

At 10:00 P.M., the same day, a marked change had taken place in the appearance of the embryos. An equal division of the macromeres had occurred, making them now eight in number; furthermore, the rounded surfaces of these cells, which had stood out so conspicuously, were now contracted and flattened, giving the whole mass a rather globular form again (Fig. 1*l*, *m*).

Owing to the thickness of the egg capsule, it was not possible to see the minute structures of the embryos without tearing open the capsule and examining the embryos in water. Being thus placed in unnatural environments, their life was usually short and their development retarded. For this reason, the time normally required for the successive steps of development cannot be correctly indicated.

At the time the micromeres became contracted and rounded off peripherally, the micromeres also pulled toward the center, crowded together, and thus, aided by their increased number, helped to restore the embryo to its former globular form. Viewed from the equator the embryo now resembled a basket full of eggs. This stage was observed July 11, at 3:00 P.M. (Fig. 1*n*).

Twenty-four hours later the embryo had become compressed at the poles and had lost its spherical form. In some, 12 macromeres could be seen, a division of the row distal of the vegetal pole having taken place. The micromeres, increasing in number, occupied a larger area of the surface and extended laterally so as to form an obtuse angle with the macromeres. The beginning of movement of the embryo takes place at this stage although cilia cannot yet be seen (Fig. 1*o*).

The following morning, July 13, an elongated form of the embryo had succeeded the former compressed one, the elongation having occurred along the equatorial plane. The micromeres, by their greatly increased number, now extended over almost the whole of the embryo, leaving but a small area of the macromeres uncovered. This was the blastula stage. The body was slightly tapered at the anterior end, where there was a small tuft of short cilia on each side. By means of these cilia the embryo was able to turn over and move backward and forward. This was the trochophore stage (Fig. 1*p*).

Twenty-four hours later, July 14, a gastrula was formed, partly by epiboly and partly by invagination of the macromeres. A constriction near the point corresponding to the vegetal pole of the ovum indicated the position of the blastopore. The micromeres, which were transparent, had become flattened and formed a layer of nearly equal thickness around the macromeres, which appeared as an inner dark mass. The archenteron appeared as a narrow fissure extending through the clear ectodermal layer and into the large yolk-laden endodermal cells. At the inner end of the archenteron, against the endodermal cells, a group of small, clear cells was seen which were probably mesodermal. The length of the embryo at this age was 0.16 mm. (Fig. 1*q*).

An important change took place in the next 24 hours. Two large, ciliated lateral lobes and a smaller median lobe with shorter

cilia developed from the ectoderm at the anterior end of the body. Directly posterior to each lateral lobe there was a clear, rounded protuberance, probably of ectodermal origin. The foot, also developed from the ectoderm, appeared as a bulky process on the ventral side, posterior to the ciliated lobes. Under it, near its base, was a short, pointed operculum, which on its inner surface was longitudinally convex and laterally concave. Also the shell had begun to form around the posterior part of the body, originating at a postero-dorsal point where it was attached to the body. Laterally and anteriorly the shell projected far out. The endodermal cells had become much distorted and had lost their symmetrical arrangement, yet retained their great size (Fig. 2*a, b, c*).

On July 17, 2 days after the above-described stage was observed, the opening of another capsule revealed larvae with well-developed shells and with an operculum as previously observed, except that it was much larger and extended beyond the foot laterally and anteriorly. Distinct eyes and otocysts were present at this stage as well as a bilobed ciliated velum, the oral lobes. This was the veliger stage, typical of the gastropod larva (Fig. 2*d, e*). Length of the shell at this stage was 0.20 mm.

After this stage changes in the embryo took place more slowly and no new phases occurred. Some of the existing features merely became more pronounced until the free-swimming stage was attained.

By July 23, after 14 days of incubation, the larvae began to escape normally from their egg cases. The ciliated oral lobes were well extended, and on the free surface of the foot a large purple area appeared. The operculum had lost much of its curvature and was large and broad, extending well beyond the foot both laterally and distally. The whole shell was pitted with shallow depressions and had a slight purplish tinge; a similar tinge was also possessed by the larva (Fig. 2*f, g, h*). At hatching the veliger shell was 0.22 mm. in length (Fig. 2*i, j, k*).

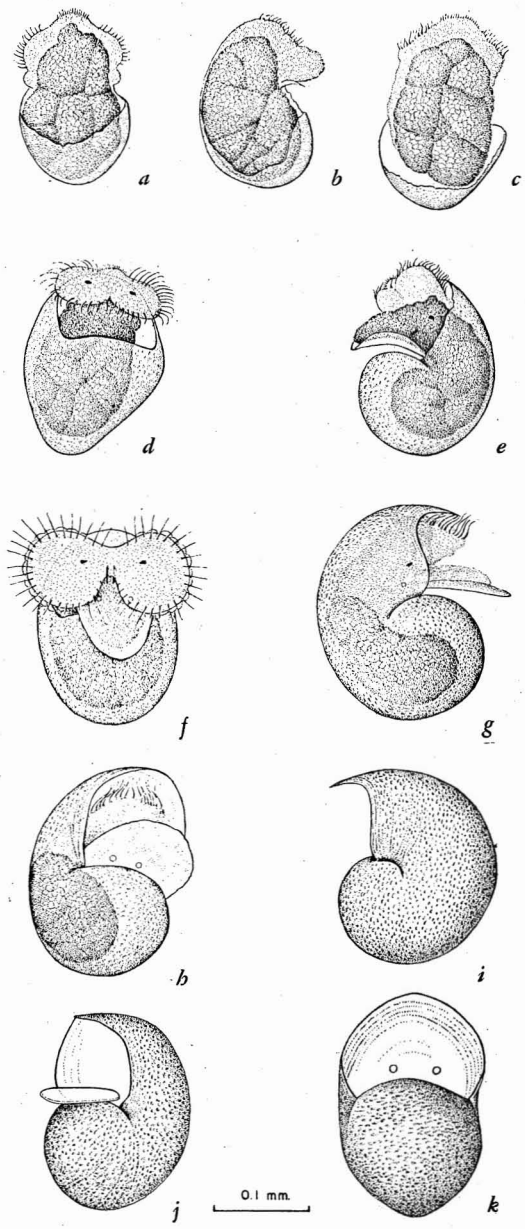

FIG. 2. *Cypraea carneola* Linnaeus. *a–c,* Early stages of shell and operculum: *a,* dorsal, *b,* lateral, *c,* ventral aspects; *d, e,* early veliger stages; *f–h,* free-swimming veliger stage: *f,* ventral, *g,* lateral, *h,* ventrolateral aspects; *i–k,* veliger shell of free-swimming stage showing operculum and otocysts.

Cypraea isabella Linnaeus

Fig. 3

During the night of July 21, 1921, a *Cypraea isabella,* which had been brought to the laboratory a few days before, deposited eggs. There were about 1,500 egg cases in three or four layers, held together by a gelatinous matrix, with the egg cases radially arranged. This egg mass, measuring about 24 x 30 mm., was fixed to the surface of a glass in which the animal was kept and was completely covered by the foot of the animal (Fig. 3*a*). The egg case was somewhat cylindrical in form, about 1.5 mm. long, pale straw color, and contained nearly 200 ova within its thick parchment wall (Fig. 3*b*).

The development of the embryo and characteristics of the veliger are very similar to those of *Cypraea carneola.* The zygote, which is smaller than that of *C. carneola,* 0.11 mm., undergoes cleavage in the same manner, and shows a corresponding difference in size of macromeres and micromeres, as well as a similar relation of these to one another (Fig. 3*c–h*). The gastrula stage is formed entirely by epiboly, the micromeres spreading completely around the macromeres. Owing to this condition no invagination is effected and the spherical form of the ovum is retained. This condition was reached after 3 days of incubation (Fig. 3*i*). In the trochophore stage, which followed, the larva assumed an elongate form and the large endodermal cells took on a distorted appearance. The foot began to develop as did the shell, which could be seen as a rudiment loosely surrounding the posterior part of the body (Fig. 3*j, k*).

The free-swimming stage was reached after 11 days of incubation, when the larva apparently had developed all the characters of the veliger stage. Between the eyes now appeared an arch of bluish-black pigment, and the foot had a large, broad operculum, as in *C. carneola*; also, as in the latter, the entire shell was covered with small, shallow pits.

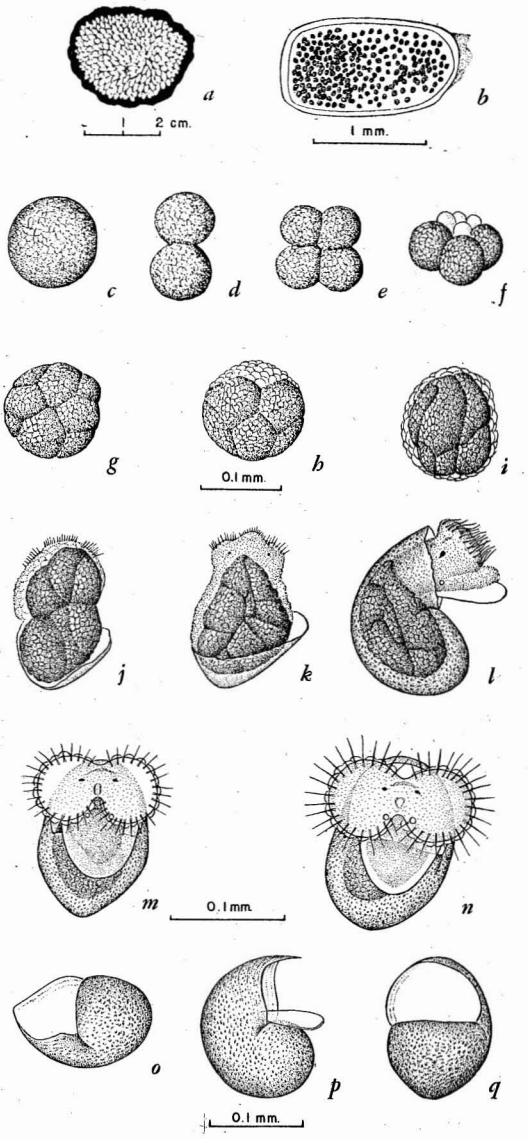

FIG. 3. *Cypraea isabella* Linnaeus. *a,* Egg mass seen through glass and covered by foot of animal; *b,* egg capsule enlarged; *c–g,* cleavage stages; *h,* blastula; *i,* gastrula; *j, k,* trochophore with shell beginning to form: *j,* ventrolateral aspects, *k,* ventral aspect; *l, m,* veliger stage: *l,* lateral, *m,* anterior aspects; *n,* free-swimming veliger; *o, p, q,* shell of free-swimming veliger showing *(p)* operculum.

The outer lip of the shell was purplish-brown; the whole shell, which was about 0.15 mm. long, had a pale tinge of that color (Fig. 3*l–q*).

Some of the larvae which survived until the ninth day of their free-swimming stage gave no evidence of metamorphosis.

Cypraea helvola Linnaeus
Fig. 4

On July 23, 1921, I obtained from a porous rock in shallow water off the laboratory two adult specimens of *Cypraea helvola,* one of which was "sitting" on an egg mass deposited on the rock.

The egg cases, or capsules, numbering about 1,000, were in many layers, imbedded in a gelatinous matrix with their long axes directed radially. The egg mass measured about 13 x 18 mm. (Fig. 4*a*).

The egg case was somewhat oval, about 2 mm. in length, of a pale straw color like those of *C. carneola* and *C. isabella,* and contained about 200 ova. The capsule walls were thinner than those of the other two and quite transparent.

Figure 4*b* shows a magnified capsule with embryos in the veliger stage.

When the egg capsules were obtained, they were found to contain embryos in the gastrula stage and were several days along in their development. The gastrulae were quite spherical and had been produced by epiboly, no sign of invagination being perceptible. The transverse measurement of the embryo in this stage was about 0.09 mm. (Fig. 4*c*).

A little later the gastrula became slightly elongate and a small tuft of minute cilia appeared on each side of the body anteriorly, as in the two preceding species (Fig. 4*d*).

In the course of 3 days these embryos became free-swimming veliger larvae, which bore a close resemblance to those of *C. carneola* of the same stage, except for being much smaller. As in that species, there was a large purple area on the ventral side of the foot (Fig. 4*e, f*).

Some of the larvae were kept in jars with standing water for about a week of their free-swimming stage without showing any perceptible change. Upon hatching they issued from the egg cases simultaneously. The cases were purple, owing to the pigment in the larvae and the transparency of their covers.

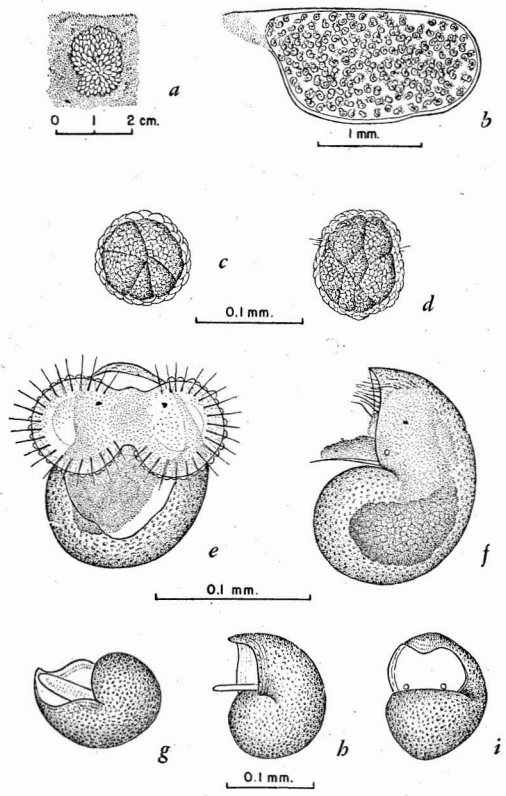

FIG. 4. *Cypraea helvola* Linnaeus. *a,* Egg mass; *b,* egg capsule enlarged with embryos in veliger stage; *c, d,* gastrula stage; *e, f,* free-swimming veliger stage: *e,* ventral, and *f,* lateral aspects; *g–i,* shell of free-swimming veliger showing operculum and otocysts.

The veliger shell measured 0.14 mm. in length, and in a number of specimens from which the dead animals had been removed by protozoan scavengers, opercula and otocysts remained. The pitted surface of the shell resembled that of the two preceding species (Fig. 4*g, h, i*).

Cypraea caputserpentis Linnaeus
Fig. 5

The commonest species of the genus in Hawaii is *Cypraea caputserpentis.* It is com-

monly encountered on the shore rocks washed by the surf during high tide. A considerable number of individuals may be seen in a comparatively small area.

The first successful attempt at obtaining the spawn of this species was made on October 26, 1920, when a specimen which was concealing an egg mass under its outspread foot was found on the shore rocks at Diamond Head. The mollusk and egg mass were taken to the laboratory for study.

The egg mass, consisting of about 100 capsules, was somewhat flattened to accommodate the animal "sitting" on it and was spread out suitably for being covered by the foot. The egg mass measured about 1 x 2 cm. through its horizontal diameters. The capsules were somewhat oblong, measured 2 mm. in length, and contained an average of approximately 200 ova.

About 1½ hours after they had been taken off the rocks, the zygotes were in early cleavage stages, having four or more cells. Subsequent investigations seemed to indicate an abnormal condition of development in which the early embryos assumed a variety of forms, many dying within the capsules. Some of the capsules ruptured in the course of 6 days, liberating embryos long before they had reached the veliger stage; in other capsules the young died. This abnormal condition possibly was caused by a faulty chemical nature of the water.

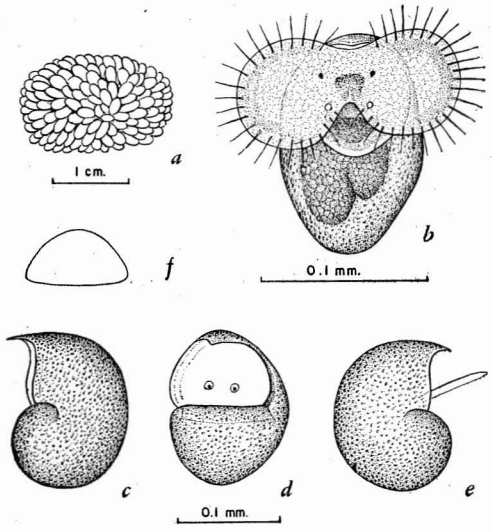

FIG. 5. *Cypraea caputserpentis* Linnaeus. *a*, Egg mass; *b*, free-swimming veliger larva, anterior aspect; *c–e*, shell of free-swimming veliger showing operculum and otocysts with otoliths; *f*, operculum in surface view.

More satisfactory results were obtained from another egg mass, also taken from shore rocks at Diamond Head. The embryos developed normally to the free-swimming veliger stage, but cleavage and embryonic development were not investigated.

The veliger larva, showing eyespots and otocysts, had a large reddish-brown area between the eyes and on the ventral surface of the foot. A similar color, but much fainter, was also present in the veliger shell, which had a pitted surface similar to that observed in each of the preceding species of the genus. A flat triangular operculum was present, and otoliths were seen, one in each otocyst (Fig. 5*a–f*).

Cypraea mauritiana Linnaeus

Fig. 6

In the morning of June 29, 1925, an egg mass was noticed in one of the aquarium tanks in which two of the mollusks were kept. The egg mass was lying on the bottom of the tank beside a rock to which it had probably been attached. Whether or not the animal had been "sitting" on the eggs, as in other cases observed, could not be said. There were about 300 egg cases in the mass. This may have been only a portion of those laid by the mollusk, inasmuch as some could have been eaten by the fishes which were also in the tank.

The egg cases were of a somewhat triangular form and attached to one another at one or more points but were not imbedded in a gelatinous substance as in other species. The egg case measured about 4 mm. in length and 3 mm. at its widest point. The capsular

wall was very thin and transparent, so that the carmine-colored ova could be seen plainly without breaking the capsule.

The ova, of which there were about 1,000 in a case, averaged 0.15 mm. in diameter. Early in the afternoon of the same day they started to divide. Most of them reached the four-cell stage by 4:00 P.M. The mode of division was the same as that observed in the other species.

Not until the seventeenth day did the larvae begin to leave the egg cases. Development had probably been retarded owing to unsuitable conditions, as many egg cases at that time contained dead embryos only.

The veliger shell, which had attained a length of about 0.235 mm., differed from those of the other species which have here been described, particularly in its sculpturing. While a pitted condition of the surface might have been recognized, closely crowded, rounded granules gave to the shell a distinctive appearance. It had a slight golden tinge, a brown columella, and margin of aperture.

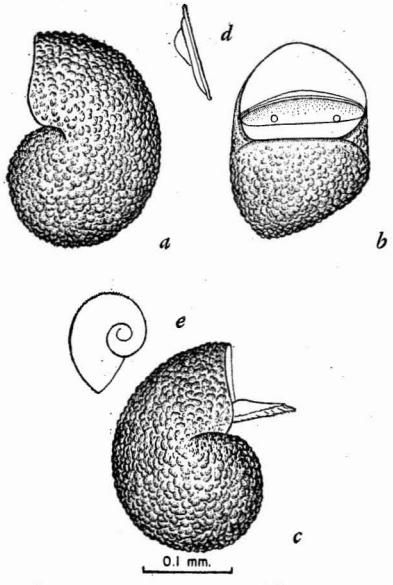

FIG. 6. *Cypraea mauritiana* Linnaeus. *a–c,* Shell of free-swimming veliger showing operculum lodged in shell; *d,* operculum in edge view; *e,* operculum showing spiral turns.

The operculum differed from those observed in the other species by being strongly convex on the surface that attached it to the foot (Fig. 6*a–e*).

Cypraea poraria Linnaeus

Fig. 7

On May 1, 1923, an egg mass of *Cypraea poraria* that was attached to a coral rock from Honolulu harbor was brought to the laboratory. The animal was "sitting" on the egg mass which, at the time it was obtained, was well along in development.

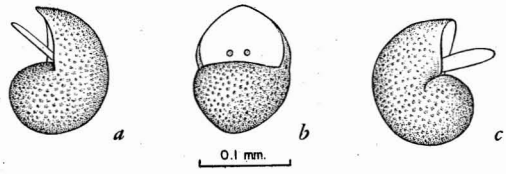

FIG. 7. *Cypraea poraria* Linnaeus. *a–c,* Shell of free-swimming veliger with opercula and otocysts.

A study was made of the veliger shell alone. This measured 0.14 mm. through its greater diameter, or length. It had a very delicately pitted surface of a pale golden-yellow coloration. The operculum, broadly rounded, was slightly concave longitudinally on its free surface (Fig. 7*a, b, c*).

PROTECTION OF EGGS BY *Cypraea isabella* LINNAEUS AND *Cypraea helvola* LINNAEUS

As I was fortunate enough to obtain eggs from species of *Cypraea* kept in the laboratory during the summer of 1921, it was possible to observe the strong maternal instinct developed in these mollusks as shown by the protection of their eggs.

Cypraea isabella deposited its egg mass on the side of the glass in which it was kept, a few days following its capture. The egg mass, consisting of about 1,500 cases imbedded in a gelatinous matrix, was spread out so as to be conveniently covered by the foot of the animal. Various interesting methods em-

ployed by this mollusk to keep an intruder away made it evident that it was greatly concerned in preventing the removal of any of its eggs.

When an attempt was made to push back the edge of the foot so as to expose the egg cases, the animal would at once move toward the disturbing object and spread out its foot in that direction. When the points of a pair of forceps were placed in front of it, near its head, it would assume an aggressive attitude and advance toward the forceps, touching them or pressing against them with its tentacles and proboscis in a determined manner. But the most striking method employed by the animal to frighten away an enemy consisted of raising the shell as high as possible and then with great suddenness bringing it downward and forward to its normal position, thereby agitating the water around it. These antics would be repeated many times when the animal was disturbed.

Since an enemy from behind or from the sides could not always be seen, the mollusk was guided by touch, to which it was very responsive. When the forceps were placed against the posterior part of the foot, the animal would move back the shell, exposing the posterior part of it by retracting the mantle lobes so the two "eyespots," which are so conspicuous in this species, became visible. Whether this had any significance or not could not be determined. The *Cypraea* did not stop at that, however, for the posterior end of the shell would be brought against the forceps in an attempt to force them away; and by means of the posterior canal of the shell, the animal was able to get a firm hold on the forceps and twist them slightly from side to side. The animal remained constantly on its eggs during the entire 11 days of incubation.

A *Cypraea helvola* with eggs, which was obtained about the same time from a coral rock on the reef, employed, with equal vigor, the methods of defense observed in the above species, with the exception that it did not seem to use the uncovered posterior end of its shell in any way. This species has no "eyespots" on its shell.

The animal remained on its "nest" until the eggs hatched and liberated the veliger larvae, upon which it promptly left, giving no further evidence of interest in its offspring.

Family *MITRIDAE*

Genus MITRA

Mitra astricta Reeve

Fig. 8

On October 17, 1921, I found the spawn of *Mitra astricta* on a rock about 25 meters from shore near the laboratory. There were three adult mollusks on the coral rock containing the eggs, one of them being very close to the egg mass, which was freshly laid. This was taken as good evidence of parentage until later verification could be furnished.

The egg cases, about 100 in number, were separately attached within a cavity of the rock, each one adhering firmly to the firm substratum of the rock by means of a tough, parchment-like base. The egg case was about 2½ mm. in length, club-shaped or oblong, and consisted of a thin, tough, fibrous capsule of a pale straw color. At the attached end this capsule was continuous, forming a stout, broad base by means of which it adhered to the rock (Fig. 8*a*). The albuminous fluid with which the capsule was filled contained from 100 to 150 ova (Fig. 8*b*).

The zygotes were 0.14 mm. in diameter and the type and rate of cleavage were similar to those that had been observed in species of *Cypraea* and *Conus*. In many instances, however, the first division resulted in unequal cleavage, but this might have been an abnormal condition. After the first division, in what appeared to be the normal, or usual, condition, the two equal-sized blastomeres contracted so as to produce an oval body of the two daughter cells. Such a contraction

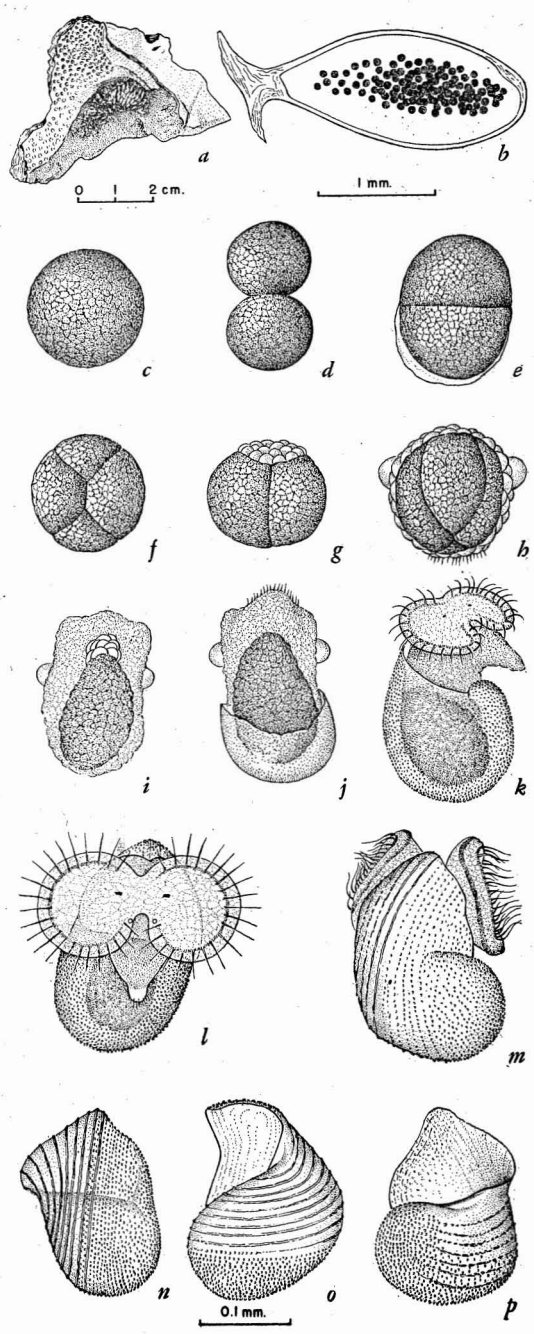

FIG. 8. *Mitra astricta* Reeve. *a*, Egg capsules attached to rock; *b*, enlarged capsule; *c–g*, cleavage stages; *h*, blastula stage; *i*, gastrula stage; *j*, embryo showing rudiment of shell; *k*, veliger; *l*, *m*, free-swimming veliger: *l*, ventral, and *m*, dorsal aspects; *n–p*, shell of free-swimming veliger larva.

of the blastomeres after the first and second divisions seems a usual condition in the gastropods, but it was more pronounced in this case than generally. Cleavage proceeded rather slowly at first, the four-cell stage having been reached only after 24 hours; the following 24 hours presented a stage in which 20 or more micromeres capped the animal pole. There were four macromeres (Fig. 8*f*, *g*).

After 3 days of development the micromeres had greatly increased in number and constituted about one-half of the surface area of the embryo; a number of those near the vegetal pole had developed short cilia, while the four large macromeres were as yet undivided. Projecting out from each side of the embryo was a large micromere, clear like the others, about half of its sphere protruding beyond the surface of the ectoderm. This stage was evidently comparable to the blastula, although the space required for the segmentation cavity was entirely obstructed by the large macromeres (Fig. 8*h*).

A day later—after 4 days' development—the embryo had become elongate and the micromeres had surrounded by a complete layer (ectoderm) the dark, conspicuous macromeres, which also had taken on an elongate form, but the boundaries of which had now become so obscure that it was impossible to determine their number. At the anterior end of the macromeres there was a cluster of rather large, clear cells, probably mesodermal. Anteriorly the ectodermal layer, in connection, perhaps, with an underlying mesoderm, had developed three slight lobes, the rudiments of the velum. Cilia could not be seen although they must have been present as the embryo showed considerable activity. This was the gastrula stage (Fig. 8*i*).

After the sixth day a shallow cup-shaped shell surrounded the posterior region of the embryo (Fig. 8*j*). Seven days of development brought out the veliger stage. A bilobed ciliated velum which had minute eyespots was found. A short pyramidal foot was

present, and a finely granulated shell surrounded the greater part of the larva (Fig. 8*k*).

From this time on, development proceeded rather slowly, no marked changes taking place until the free-swimming stage was reached, after 14 days of incubation. The velum consisted then of two circular lobes with a double line of purplish-pink around the borders. Eyes and otocysts were present. The foot terminated in a blunt translucent tip set with bristles. The operculum was observed in only one specimen and was small and rudimentary (Fig. 8*l, m*). The first whorl of the shell started with a corkscrew spiral as in the common snail. The apex was sprinkled with granulations which tended to be in rows distally; while the distal half of the veliger shell was ornamented with granular spiral ridges. These ridges seemed to correspond to the transverse striae on the whorls of the adult shell. The shell was colorless and about 0.22 mm. long (Fig. 8*n–p*).

Mitra auriculoides Reeve

Fig. 9

On December 21, 1923, while collecting on the reef about 15 meters offshore near the laboratory, I found a group of egg cases attached to the undersurface of a rock, accompanied by a *Mitra auriculoides.* There could hardly be any more doubt that the egg cases belonged to this mollusk than in the case of *Mitra astricta* obtained 2 years before under similar circumstances. Furthermore the comparison of egg capsules, veliger larvae, and shells bore out this conclusion.

The egg cases, about 100 in number, were crowded closely together and occupied nearly 2 square cm. of the rock surface. The egg case, resembling greatly that of *Mitra astricta,* was club-shaped, about 4 mm. in length, and was attached to the rock at one end by a basal extension. The capsule wall was very thin and there were about 200 ova to the capsule.

When the egg mass was found the capsules contained embryos in an advanced veliger stage, the coloring of which imparted a pale brownish tinge to the capsule (Fig. 9*a, b*).

On December 28, the young escaped from their enclosures, and the close resemblance to both larva and shell of *M. astricta* was obvious. The same double band bordering the veliger lobes was present, and the ridges and granulations on the shell were distributed as in the other species. The operculum, however, showed a marked difference; while it was almost absent in *M. astricta,* it was well developed in this species. The foot was pro-

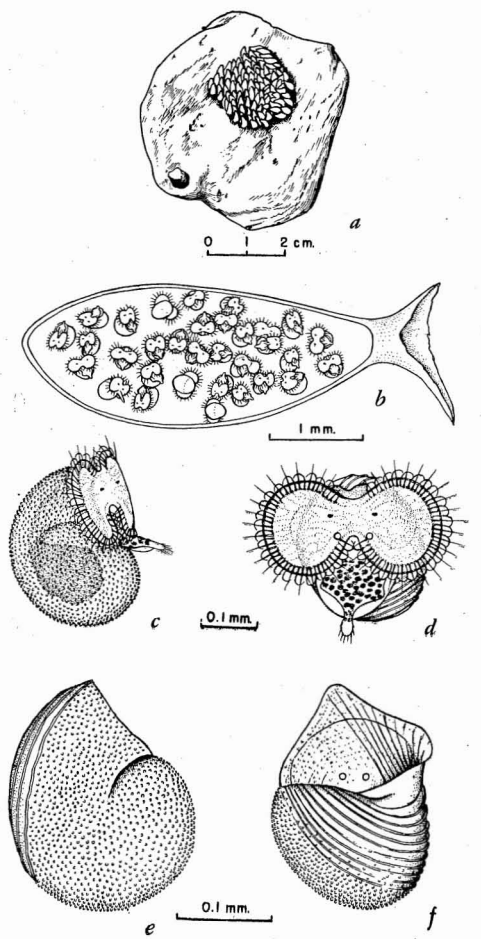

FIG. 9. *Mitra auriculoides* Reeve. *a,* Egg capsules on rock; *b,* magnified capsule with embryos in veliger stage; *c, d,* free-swimming veliger; *e, f,* shell of free-swimming veliger.

duced laterally into two angular processes, and anteriorly, as in *M. astricta,* into a blunt, rounded process with bristles. Eyes and otocysts were present. The marginal bands on the velum were greenish-brown. Numerous spots of the same color occurred also on the foot. The length of the shell was 0.25 mm. (Fig. 9*c–f*). The larvae showed a strong positive phototropism.

Family *CONIDAE*

Genus CONUS

Conus tahitensis rattus Hwass

Fig. 10

While collecting on the outer reef near the Elk's Club at Waikiki during the morning of August 4, 1921, I picked up a specimen of *Conus tahitensis* in the act of depositing eggs. I broke off the rock to which the egg capsules were attached and took it to the laboratory.

There were 22 egg cases of a soft, thin structure and of a comparatively large size, about 11 x 15 mm. Each egg case contained about 2,000 ova of rather small size, 0.125 mm. (Fig. 10*a*).

The ova, in respect to distribution of yolk (deutoplasm) and cytoplasm, agreed closely, insofar as could be observed without special preparations, with those of *Cypraea* and *Mitra.*

The early stages of cleavage were observed in a capsule about 6 hours after deposition. The first division resulted in two cells of equal size. These rounded out independently until the two cells were joined to each other by a very small area. Soon they contracted toward each other to assume the appearance they had before the first division was complete (Fig. 10*b, c, d*). The second division, resulting in four cells of equal size, had occurred about 1 hour after the first. Here again, as in the first division, the cells were rounded off and standing out prominently.

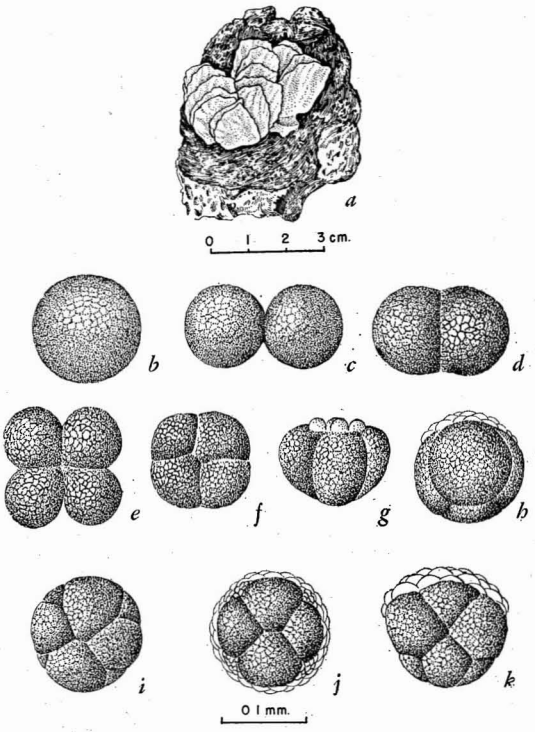

FIG. 10. *Conus tahitensis rattus* Hwass. *a,* Egg capsules attached to rock; *b–k,* cleavage stages from the ovum to the blastula stage.

These again became pulled toward the center, so that the entire mass became neatly spherical (Fig. 10*e, f*). The next cleavage was unequal, resulting in four micromeres and four macromeres, as in *Cypraea* and *Mitra* (Fig. 10*g*). Succeeding cleavages resulted in a cap of micromeres at the animal pole. The macromeres now divided nearly equally into four cells of lesser size which came to lie at the equator, and four larger ones which surrounded the vegetal pole. The micromeres soon extended to the equator, covering half of the sphere of the embryo and projecting out beyond the macromeres (Fig. 10*h, i, j*).

This was the blastula stage and the embryo now began to show activity. It appeared that in some of the embryos another division of the four equatorial macromeres had taken place, as some embryos had 12 macromeres

This was also observed in *Cypraea carneola* and is probably a common condition (Fig. 10*k*). Owing to the loss of all the larvae, no further observations on the development were made.

In February, 1923, another *Conus tahitensis* with egg capsules was found near the laboratory. The egg capsules were much smaller, but agreed in other respects with the one described, i.e., in color, texture, number, and size of ova. As in the previous lot none developed beyond the blastula stage.

Conus omaria Hwass

Fig. 11

On May 19, 1921, I found, near the laboratory, a number of *Conus* egg cases which were attached to the underside of a rock. Under this rock also was an adult *Conus omaria,* a rather rare species on this reef. The egg capsules differed from all those previously observed in that only a few of them were attached directly to the rock; the greater number, about 34 in all, were joined to one another, forming arches and bridges (Fig. 11*a*).

Upon examining the contents of one of these capsules, I found zygotes in very early cleavage stages. Some were still unsegmented, while a number were in the two-cell stage, the result of an equal division. A few had undergone a second division which was equal, four blastomeres of a smaller size resulting.

The capsules of this species, measuring about 11 mm. in length and 8 mm. in width, contained a small number of large ova, 0.47 mm. in diameter, often less than 50 in one capsule. The zygotes failed to develop when removed from the capsule, so it was necessary to open one each day to follow their progressive development. Five days after they were obtained some of the embryos had begun to form a shell. And after 11 days of incubation they had attained well-advanced stages, a large shell having formed about the

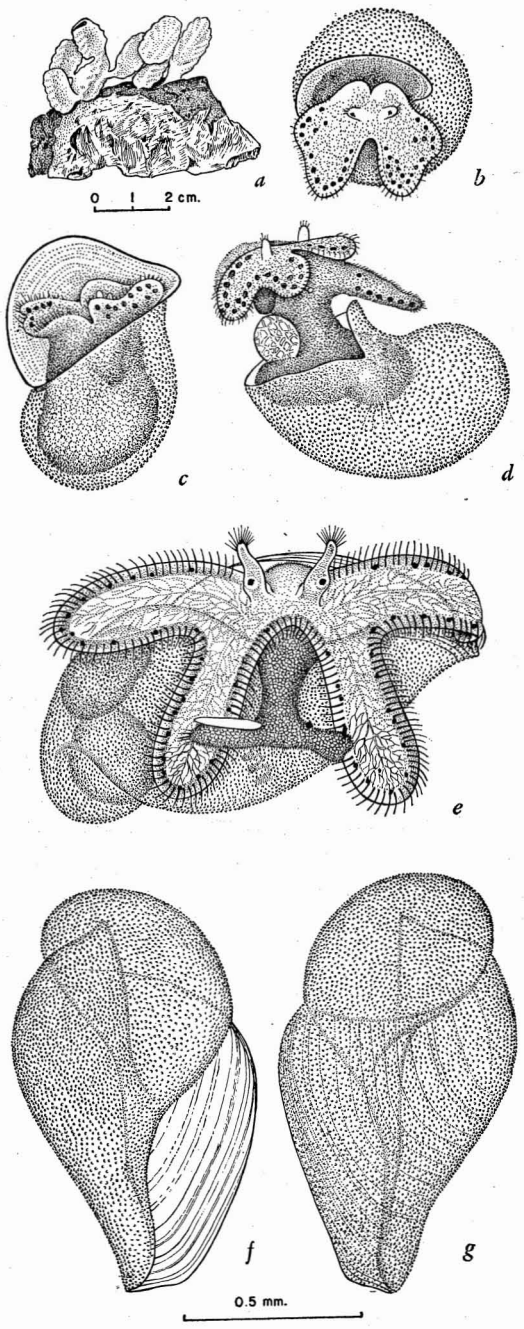

FIG. 11. *Conus omaria* Hwass. *a,* Egg capsules attached to rock; *b–d,* stages of development in veliger larva, heart showing as a globular body in *d*; *e,* veliger larva after normal release from capsule; *f, g,* shell of veliger larva.

body. The veliger lobes had also attained a large size, yet the cilia bordering them remained short. The heart could be seen distinctly as a single-chambered oval bag on the dorsal side posterior to the veliger lobes. Its alternate contraction and expansion would change its volume about 100 per cent. The large veliger lobes were bordered by a single row of yellowish pigment cells. A pair of blunt papilla-like tentacles supporting the eye were tipped with a few short bristles. The shell showed a fine granulation. No operculum was present on the large foot (Fig. 11*d*).

At the sixteenth day of incubation some changes were noticeable. The two veliger lobes had developed greatly, each having a deep lateral indentation. The cilia also had increased greatly in size and were beating rhythmically, keeping the animal upright with the apex of the shell against the bottom. The large bilobed foot supported a small operculum on one of its lobes and was covered with very fine cilia; a few prominent bristles were present at its opercular end. Two prominent tentacles, bearing the eyes on basal swellings and beset at their extremities with a large tuft of bristles, occupied a central position on the veliger lobes (Fig. 11*e*).

At this stage, 16 days of incubation after the beginning of cleavage, the larvae began to escape into the water, but, unlike those of other species here observed, they remained within the albuminous substance of the capsule which had been discharged into the water and did not attain the power of swimming at any time while under observation. This inability to swim may be ascribed to the great size and weight of the shell, some of the veliger shells having attained a length of over 1.25 mm. with about one and a half volutions (Fig. 11*f, g*). A fine granulation covered its entire outer surface, which had taken on a faint golden tinge, most pronounced anteriorly. The columella seen through the quite transparent shell had a pale rose tinge. This coloration of the veliger shell is an approach to that in the shell of the adult.

Egg capsules corresponding to those of *Conus omaria* were found near the Marine Laboratory, May 25, 1922, but were of a larger size than the first lot. These capsules contained advanced veligers, one capsule containing about 40, another as many as 150 embryos. Some of the larvae of this lot were kept for over a week after their escape from their capsule without ever showing signs of swimming. Some, however, would drag their shells on the bottom of the dish by means of the propelling force of their velar cilia. A number of the larvae were normally expelled from the capsule, which seemed to be effected by a dissolution of the "window" at the free, or distal, end of the capsule, followed by a contraction of the capsular walls, resulting in a squeezing out into the water of the albuminous substance containing the larvae. It may be that both chemical and mechanical agents are responsible for this occurrence, and that the larvae, at the time of their liberation, emit some secretion which brings about the desired results.

A circumstance which might be correlated with the absence of a free-swimming stage of this species is the fact that *Conus omaria* occurs in many varietal forms in various parts of the Hawaiian Islands; so much so that some authorities are inclined to consider some of them distinct species.

One might suppose that the free access to widespread areas possessed by those species having such an efficient mode of dispersal as a pelagic veliger larva would serve to break down varietal strains which might be in process of development and thus tend to stabilize the species, whereas an immotile larva, as here observed in *Conus omaria,* would have the opposite effect.

Conus catus Hwass

Fig. 12

On June 12, 1922, a mass of egg capsules

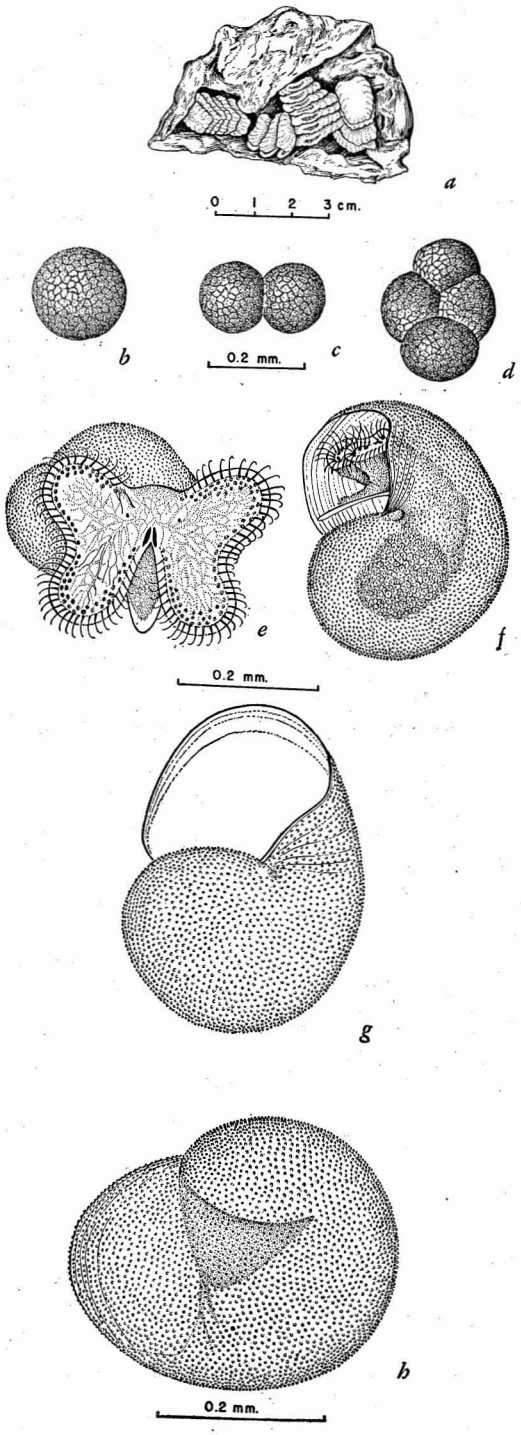

FIG. 12. *Conus catus* Hwass. *a,* Egg capsules attached to rock; *b–d,* cleavage stages; *e, f,* free-swimming veliger larva; *g, h,* veliger shell of free-swimming larva.

attached to a rock with a *Conus catus* beside it was found near the Marine Laboratory. These capsules, of a pale straw color, were thin, semi-transparent, yet firm and rigid, measuring about 9 x 12 mm., and containing from 500 to 1,000 ova (Fig. 12*a*).

The diameter of the zygotes averaged 0.2 mm., and cleavage was similar to that observed in other species of the genus, i.e., equal in the first and the second division, unequal in the third (Fig. 12*b, c, d*).

The larvae attained the free-swimming veliger stage in 15 to 16 days, at which time the shell measured about 0.375 mm. in length. The velar lobes were of medium size with a lateral indention which partly divided them, but to a far less extent than in the veliger of *C. omaria.* The lobes were bordered by a continuous line of many pale green pigment spots which were increased in number at the extremities of the lobes so as to form two or three rows. Eyes were distinct with a rather short tentacle at the right eye. The mouth was marked by an elongate black streak on each side. The foot was somewhat narrow and pointed, bearing an operculum which extended well beyond it distally. Fine bristle-like processes were present (Fig. 12*e, f*). The shell was ovate and densely granulate, consisting of about one spiral turn. Some of the shells had a faint reddish tinge on the outer lip (Fig. 12*g, h*).

Conus hebraeus Linnaeus

Fig. 13

On March 22, 1921, a *Conus hebraeus* kept in the laboratory in a pan of water was found in the act of laying an egg case. Further inspection of the pan resulted in the discovery of other cases. The egg case being laid was partly held by the animal and was of a jelly-like consistency. Upon contact with the water, the capsular walls gradually hardened and it assumed the appearance of the other egg cases. The capsules were very pale straw-

colored with corrugated distal margins. They were almost square and measured about 10 mm. across (Fig. 13*a*).

Cleavage was not investigated in this species. After a period of 9 days the embryos had begun to show activity, short cilia having developed in three regions near the anterior end of the body. A shell had also begun to form, taking the form of a slipper, and beginning, apparently, at a dorsoposterior region of the body of the embryo, at which place it was attached (Fig. 13*b, c*). As growth of the shell progressed, it spread to the side, becoming cup-shaped. This stage was observed 1 day later (Fig. 13*d, e*).

In the course of 24 hours an interesting transitional stage occurred. The lateral ciliated areas constricted to form veliger lobes. The cilia grew rapidly and other cilia appeared along the borders of the lobes; the anterior cilia remained short, as did those now visible on the foot. The veliger lobes gradually unfolded and the embryo began to assume the appearance of the free-swimming form. The shell covered the greater part of its body.

The embryo quickly grew into the free-swimming larva as the veliger lobes were completely unfolded and the cilia became capable of propelling the animal through the water. Since simultaneous development of the embryos in the capsule is not the rule, a provision seems to have been made for those that have been retarded in that the capsule does not expel its contents of young in favor of a minority, but remains closed until the great majority have reached the stage where the new environment becomes imperative.

At the free-swimming stage the rather orbicular veliger lobes were bordered with a row of pale-green pigmented cells; bristles projected from the tip of the ciliated foot, which was without an operculum and pointed. Eyes were present. The shell, measuring 0.28 mm. in length, bore a fine granulation (Fig. 13*f, g*).

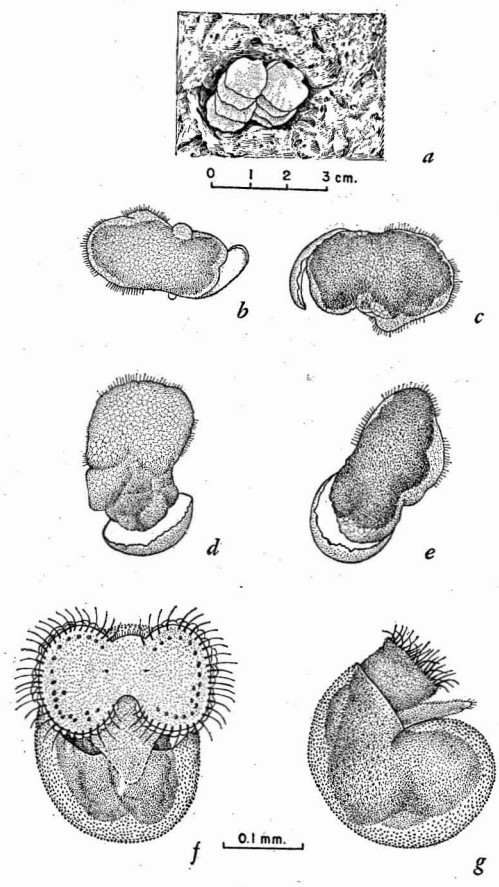

FIG. 13. *Conus hebraeus* Linnaeus. *a,* Egg capsules attached to rock; *b, c,* trochophore larvae showing beginning of shell formation after 9 days of incubation; *d, e,* trochophore stage after 10 days incubation; *f,* free-swimming veliger, ventral aspect; *g,* free-swimming veliger, lateral aspect.

Conus sumatrensis Hwass

Fig. 14

May 16, 1921, while collecting about 50 meters off the Marine Laboratory, I found a group of 34 egg cases of *Conus* attached to the lower side of a piece of coral, and right beside them was a *Conus sumatrensis.* Inasmuch as the zygotes were in very early stages of cleavage, there could be little doubt as to their identification.

The egg cases, quite unlike those of other known species of *Conus* described in this paper, are very soft and thin; they average

13 x 20 mm. Thousands of ova, which in this species were quite small (0.14 mm.), were contained in a capsule (Fig. 14*a–d*). Early cleavage stages only were observed. Numerous polar bodies were seen with them.

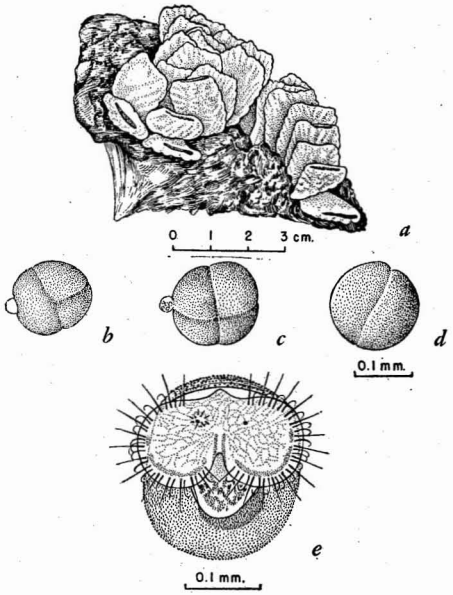

FIG. 14. *Conus sumatrensis* Hwass. *a,* Egg capsules attached to rock; *b–d,* cleavage stages showing polar bodies; *e,* free-swimming larva, ventral view.

After 4 days of incubation the embryos began to show activity and a shell had begun to form. After 7 days the anterior end of the embryo had assumed a trilobular form with short cilia. A shell covered the greater part of the body. On the twelfth day of incubation the young began to leave their capsules, entering upon their free-swimming larval stage. The veliger lobes were rounded and pigmented with green as in *C. hebraeus,* but unlike the larva of that species, a rounded foot, with an operculum projecting beyond it, was present. The shell, which measured 0.25 mm. in length, was covered with a fine granulation (Fig. 14*e*).

Conus abbreviatus Nuttall
Fig. 15

On March 15, 1923, a dozen egg capsules

FIG. 15. *Conus abbreviatus* Nuttall. Egg capsule attached to rock.

were deposited by a *Conus abbreviatus* which had been isolated in the laboratory. The capsules averaged 8 x 10 mm., had firm and rigid walls with smooth sides and margins, except for the distal margins, which were slightly corrugated (Fig. 15). A slight reddish tinge was discernible. Cleavage and larval development were not investigated.

The egg capsules of *Conus* have not been of uncommon occurrence in the shallow water of the Waikiki reef near the Marine Biological Laboratory. Several different forms have been found and specific distinction could often be made by the differences in size, shape, and firmness, and perhaps to some extent by color. A comparison between ova and veliger larvae of a few unidentified capsules, with ova and veligers of determined species, has shown a corresponding distinction. In other words, specific characters may be recognized in the egg capsules.

The capsules in all the species under observation had tough parchment-like walls with more or less corrugated borders. A slit through which the young might escape when they reached the free-swimming stage was present at the distal end of the capsule. During incubation this slit was closed by a clear, semi-transparent substance which then appeared as a window. My observations have not convinced me that the young may not also be released by a rupture of the capsule.

The following species of *Conus* have been found in the living state within wading distance of the Marine Laboratory:

C. abbreviatus Nuttall
C. catus Hwass
C. flavidus Lamarck

C. hebraeus Linnaeus
C. imperialis Linnaeus
C. lividus Hwass
C. miles Linnaeus
C. nanus Broderip
C. omaria Hwass
C. sumatrensis Hwass
C. tahitensis rattus Hwass

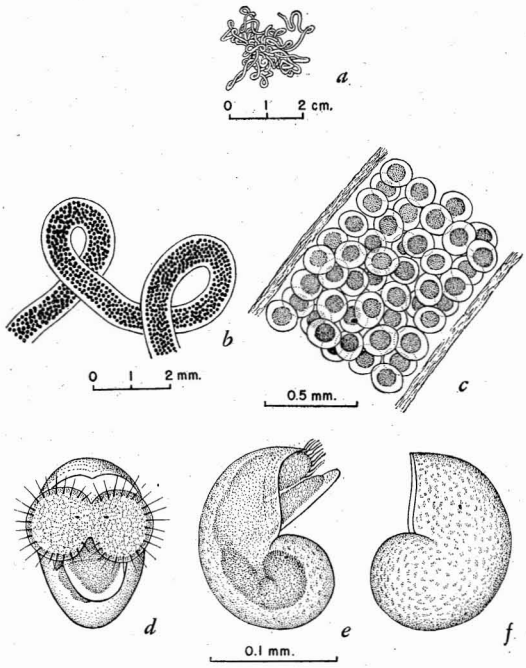

FIG. 16. *Clava obeliscus* (Bruguiere). *a,* Egg filament; *b,* portion of filament enlarged; *c,* section of filament highly magnified; *d, e,* free-swimming veliger larva: *d,* ventral, and *e,* lateral aspects; *f,* shell of free-swimming veliger.

Family *CERITHIDAE*

Genus CLAVA

Clava obeliscus (Bruguiere)

Fig. 16

An egg filament of *Clava obeliscus* was deposited in a dish by a specimen of the mollusk on March 28, 1922.

The egg structure was a pale cylindrical filament about 0.75 mm. in diameter, twisted and coiled upon itself to form a tangled mass. The parchment-like walls of the filament were thick and fibrous. The filament contained a closely packed mass of ova, lying about five abreast in cross section. The ovum, measuring about 0.9 mm. in diameter, was surrounded by a hyaline membrane whose diameter was about twice that of the ovum (Fig. 16*a, b, c*). Development was not investigated. The embryos reached the free-swimming veliger stage in the short period of 6 days. The larva was of a pale straw color. Eyes were present, as well as otocysts; the veliger lobes were rather small, but the operculum was large and rounded. The shell was about 0.16 mm. in length and slightly pitted, much resembling that of the *Cypraea* veliger (Fig. 16*d, e, f*).

Family *STROMBIDAE*

Genus STROMBUS

Strombus maculatus Nuttall

Fig. 17

In a dish containing two specimens of *Strombus maculatus* several egg structures were deposited on March 16, 1922. These egg structures, which were lying unattached on the bottom of the dish, consisted of a

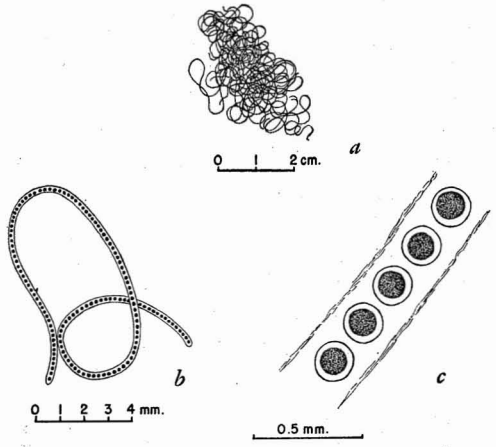

FIG. 17. *Strombus maculatus* Nuttall. *a,* Egg filament; *b,* filament enlarged; *c,* section of filament highly magnified.

maze of very fine pale-yellow threads of various lengths, tangled and glued together as if they were one continuous coil. When magnified, the thread proved to be a cylindrical gelatinous tube with a single row of ova placed in its center and strung out like a single strand of beads, each ovum being surrounded by a globular membrane.

The diameter of the filament was about 0.25 mm., that of the membrane 0.13 mm., and that of the ovum about 0.10 mm. (Fig. 17*a, b, c*). The zygotes died at the morula stage.

Family *MURICIDAE*

Genus MORULA

Morula dumosa (Conrad)

Fig. 18

On July 1, 1923, an egg filament was laid in the laboratory by a specimen of *Morula dumosa* which had been kept for some time. This was a white, cylindrical filament of about two volutions and of about 25 mm. in length. The walls of the coil were fairly thick and the cavity was packed with ova. Each ovum was enclosed in a hyaline envelope of a circular to oval shape, the ovum within measuring about 0.03 mm., therefore among the smallest recorded in this paper (Fig. 18*a, b*).

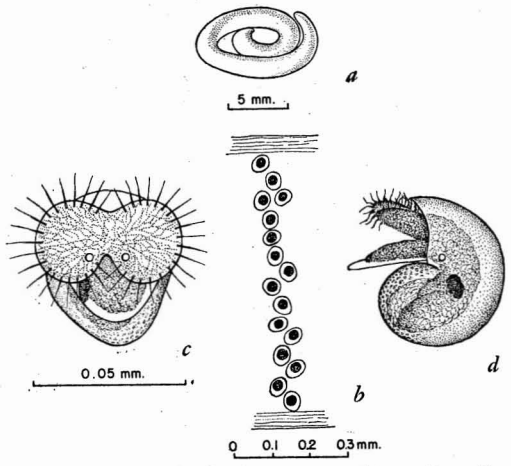

FIG. 18. *Morula dumosa* (Conrad). *a*, Egg filament; *b*, section of filament magnified; *c, d*, free-swimming veliger larva: *c*, ventral, and *d*, lateral aspects.

The free-swimming veliger larva was of a pale-brownish tinge with a large black pigment spot near the base of the foot. Otocysts were present but not eyes. The veliger lobes were round and bore large cilia. Foot and operculum were well developed (Fig. 18*c, d*).

Family *DOLIIDAE*

Genus TONNA (= DOLIUM) (Linnaeus)

Tonna perdix (Linnaeus)

Fig. 19

On June 22, 1924, Ted Dranga, an experienced diver and collector of marine organisms, located near Kapapa Island, Kaneohe Bay, what appeared to be the egg structure of *Tonna perdix.* There were several of these structures about 3 meters from a group of the mollusks. The largest egg structure was nearly circular in form with a diameter of about 15 cm. and with a thickness of about 2 mm. An indentation of about 6 cm. occurred at one side, by which the structure had its attachment, so the form of it is not unlike that of a leaf of a pond lily.

Within the thick parchment walls were 3,076 egg envelopes, neatly arranged in semicircular rows. These egg envelopes were cylindrical with rounded ends, measured about 1 x 2 mm., and contained an average of 49 ova. An estimate of the number of ova in the total structure is 150,724. The ova were rather large, averaging about 0.30 mm. in diameter, and were grouped together within their envelopes so as to form elongate masses with a constriction at the middle. They had a pale-orange tinge (Fig. 19*a, b*).

When the egg structures were brought to the laboratory, the zygotes were in early stages of cleavage. Some were probably in the morula stage, having four macromeres

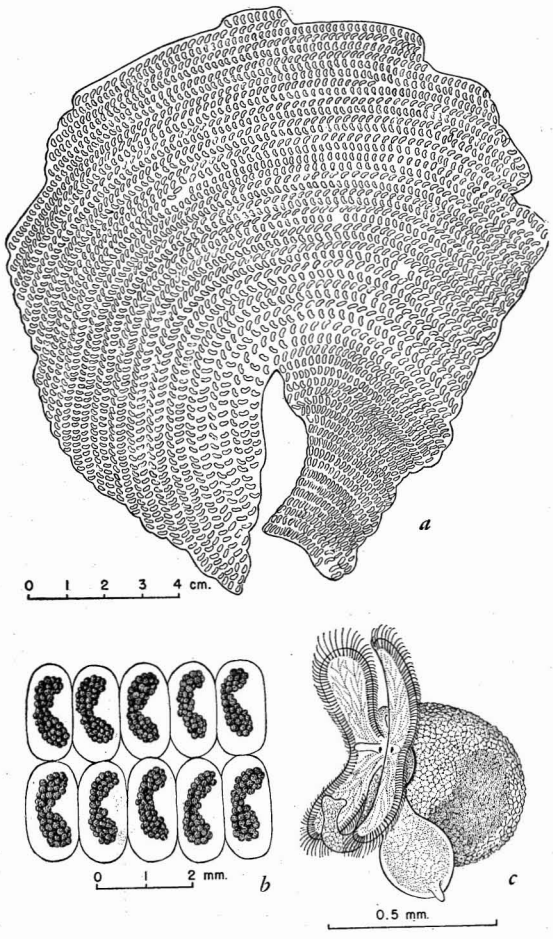

FIG. 19. *Tonna (= Dolium) perdix* (Linnaeus). *a,* Egg structure; *b,* egg envelopes with grouped masses of ova; *c,* free-swimming veliger larva showing a prominent proboscis.

and numerous micromeres, the latter reaching about to the equator. A day or two later a stage in which the embryos showed a slight amount of movement was attained. This was probably the blastula stage, the segmentation cavity being occupied by the large macromeres.

The length of time required for the larva to become a free-swimming veliger was not recorded. At this stage the larva was provided with large veliger lobes, eyes, a long proboscis, and a rounded foot with an operculum extending beyond its borders. A pale-yellow color was seen in the animal's visceral mass. The shell, measuring 0.55 mm. in length, was covered with a fine reticulum of slightly elevated polygonal areas (Fig. 19*c*). It was tinged with carmine along the margin.

It is of interest to compare the egg structure and larva of this species with those of one recorded from the Iranian Gulf by Gunnar Thorson (1940: 192–195).

Family *LITTORINIDAE*

Genus LITTORINA

Littorina pintado Wood

Fig. 20

A large quantity of eggs was obtained from a number of specimens of *Littorina pintado* which were kept in a glass of water in the laboratory. The eggs were deposited during the night and in the morning were found scattered in profusion over the bottom of the glass.

Each ovum, contained within a hyaline membrane, was usually enclosed in a capsule alone; rarely two or more ova were present. The capsules were somewhat globular or pyriform, flat on one surface and convex on the other with a transverse diameter of the flat

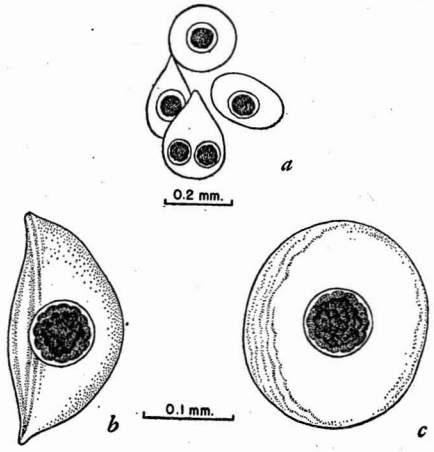

FIG. 20. *Littorina pintado* Wood. *a,* Egg capsules enlarged; *b, c,* egg capsule magnified, and seen from edge and flat surface.

surface of about 0.19 mm. The ovum measured about 0.08 mm. (Fig. 20*a, b, c*). Development of the ova was not investigated.

It is of interest to compare the egg capsules and ova of this species with those of two other species of the genus from Bermuda, which have been recorded by Dr. Marie V. Lebour. They are *L. zigzac* Dillwyn (Lebour, 1945) and *L. neritoides* (Lebour, 1935).

Order OPISTHOBRANCHIATA
Suborder TECTIBRANCHIATA
Family *APLYSIDAE*

Genus TETHYS (= APLYSIA)

Tethys (= Aplysia) grandis (Pease)
Fig. 21

On November 9, 1920, two egg filaments of *Tethys grandis* were found beside the Marine Laboratory pier adhering to a stone under which were two of the animals. Since then numerous filaments have been seen on the loose stones at the same place, to which the mollusks come in large numbers. They were especially abundant during the months of November, December, and January, which seemed to be the main spawning season. They were also present at other times of the year, in August for example, and their spawn would invariably be found with them.

The filament of this mollusk resembled a very tangled bundle of yellow thread with a circumference of about 15 cm. and a thickness of about 3 cm. It was supplied with thick walls and contained masses of oval or rounded hyaline membranes packed together throughout its length. These hyaline membranes lay 3 or 4 abreast in the filament and each contained 7 to 15 ova (Fig. 21*a, b*).

Early stages of cleavage were investigated in different filaments of the species. In one instance, the first cleavage was equal, the second unequal and resulted in two smaller blastomeres asymmetrically placed. This would indicate spiral cleavage. The ovum measured about 0.085 mm. (Fig. 21*c–f*).

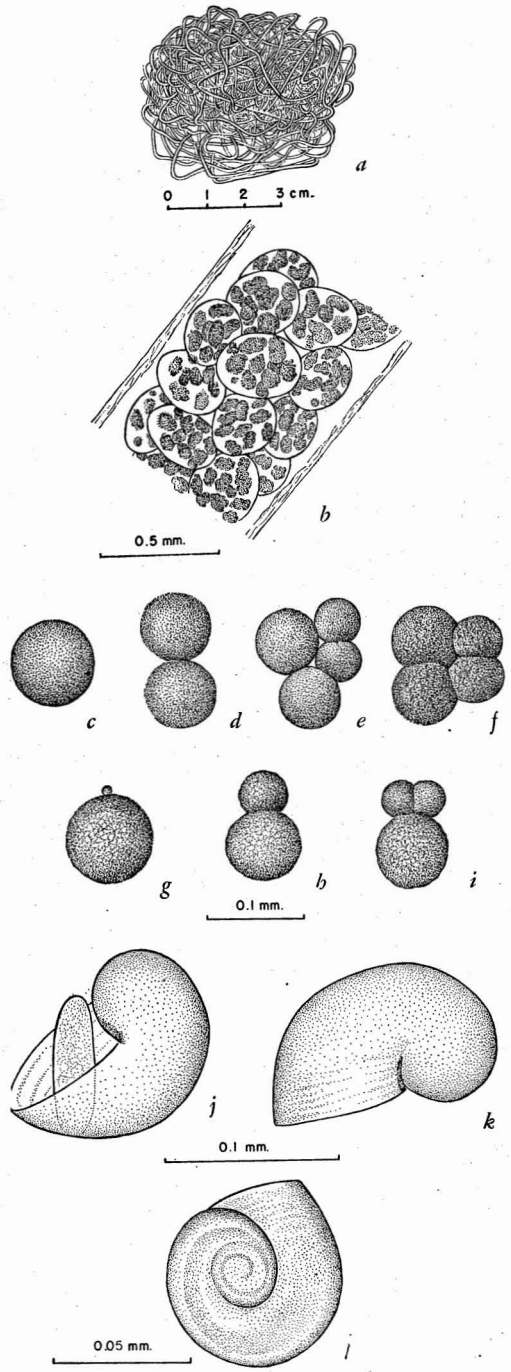

FIG. 21. *Tethys (= Aplysia) grandis* (Pease). *a*, Egg filament; *b*, magnified section of filament with active embryos; *c–f*, first type of cleavage; *g–i*, second type of cleavage; *j*, *k*, shell of free-swimming veliger stage showing operculum *(j)*; *l*, operculum more highly magnified.

A month later in the season another type of cleavage was observed in which the first was unequal and the second resulted in an embryo with three blastomeres, only the smaller blastomere of the first division having divided (Fig. 21*g, h, i*).

The total period required for incubation was not recorded. The free-swimming larva was provided with a coiled shell and a large, rounded operculum (Fig. 21*j, k, l*). The free-swimming veliger larvae were kept 21 days in a large glass container in the laboratory. During this period no indication of metamorphosis into the adult condition was discernible; only a slight growth of the shell could be detected.

After several days of incubation the hyaline envelopes within the filaments could be seen to contain a whirling mass of embryos in various stages of development, as well as zygotes in early cleavage stages. The obvious effect of this action seemed to result in the survival of the stronger and more advanced embryos over the weaker and retarded individuals, which were knocked to pieces and consumed by the stronger. Thus, a form of cannibalism existed (Fig. 21*b*).

Inasmuch as this mollusk is of quite common occurrence inshore during the cooler season of the year and is a very prolific egg layer, its spawning habit could be observed in the laboratory, where several of the animals were kept in a trough with running water in which a number of coral rocks were placed which bore algae and other marine organisms.

When the animal deposited its filament, it mounted the rough surface of a coral rock and placed the right side of its head against the surface of the rock, bringing the adhesive filament into contact with it. The filament passed along the genital groove between the parapodial lobes on to the right side of the head.

As the filament was extruded, the animal turned its head from side to side in a desultory fashion with the result that successive loops formed an irregular, tangled, thread bundle adhering to the rock. One such filament was found to have a length of 5.25 meters when it was unraveled. It contained an estimated number of ova reaching the high figure of 742,720.

Freshly deposited filaments were pale yellow, but as the embryos developed the filaments became quite brown. Under favorable conditions of development, the free-swimming young were seen to escape simultaneously in great swarms, the egg filament being literally torn to bits.

Tethys (= Aplysia) bipes (Pease)
Fig. 22

Like the preceding species, this large form occurred commonly under loose stones along

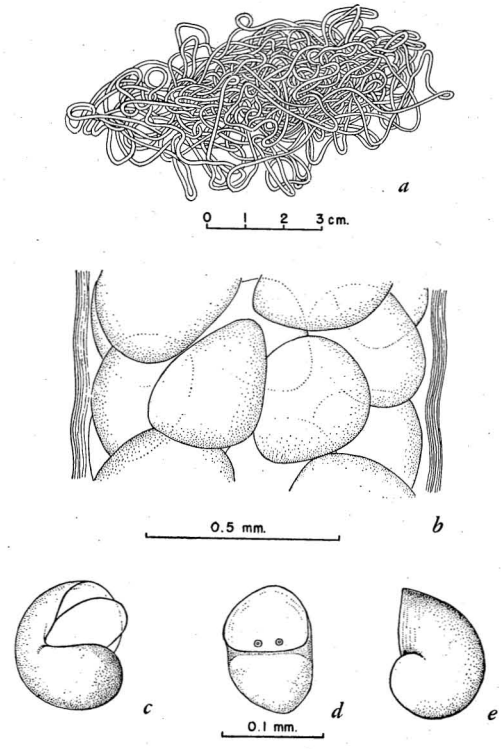

FIG. 22. *Tethys (= Aplysia) bipes* (Pease). *a,* Egg filament; *b,* section of filament magnified to show egg envelopes; *c–e,* shell of free-swimming veliger showing operculum and otoliths.

the shore during the cooler months of the year, at which time its filaments were also found in abundance. As in the preceding species the fresh filament was white or pale yellow and, as development of the young progressed, it turned to a yellowish-brown.

The structure of the filament and the type of cleavage agreed in nature with those of *T. grandis*. However, a note on the veliger shell is of interest. The shell measured about 0.125 mm. in length and consisted of about one volution, was a light golden-brown in color, darkest along the columellar line. The operculum was large and round as in *T. grandis*. Otoliths appeared distinctly within the otocysts (Fig. 22*c, d, e*).

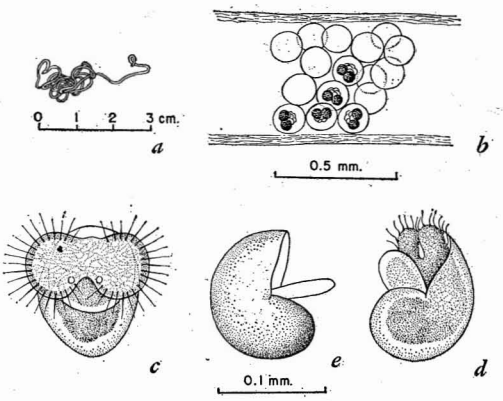

FIG. 23. *Tethys (= Aplysia) elongata* (Pease). *a,* Egg filament; *b,* magnified section of filament with early cleavage stage; *c, d,* free-swimming veliger larva; *e,* shell with operculum of free-swimming veliger.

Tethys (= Aplysia) elongata (Pease)

Fig. 23

Early in March, 1923, a specimen of *Tethys elongata* found near the Elk's Club, Waikiki, was brought to the laboratory. This animal was in general of a much darker color than the species but otherwise seemed to agree and might be considered a color variety. Two months later five more specimens like it were found in the same location.

An egg filament was deposited by this mollusk in the laboratory. This was a pale green, tangled, cylindrical filament of about 0.5 mm. in diameter. The lumen of the filament was closely packed with globular hyaline capsules with an average diameter of 0.125 mm., lying about four abreast in a cross section and each containing one ovum.

The first cleavage of the zygote was usually equal, while the second was unequal, resulting in two micromeres and two macromeres. The micromeres soon divided, giving the embryo its triangular appearance, corresponding, perhaps, to the morula stage (Fig. 23*a, b*).

The free-swimming veliger stage was reached in 11 days, and the larva then, quite colorless, was provided with otocysts but with no eyes. The shell, which was about 0.125 mm. in length, had a golden tinge and a reddish columellar region. A well-developed operculum was present (Fig. 23*c, d, e*).

Genus DOLABRIFERA

Dolabrifera olivacea Pease

Fig. 24

For a long time I sought in vain for the spawn of this mollusk, so common under loose, flat, shore rocks. Finally on February 18, 1922, an animal that was kept in a glass jar laid a peculiar, flat egg ribbon.

Later in the season—on May 25—I found, on the underside of a number of concrete slabs to which the mollusks were clinging, many of their ribbons. This egg structure is easily overlooked as it is clear and colorless—a flat band with the flat side attached to the smooth surface of a rock or other object, and spread out so as to cover a surface of 5 or more square centimeters. The ribbon rarely overlapped, but was often spread out so neatly that it formed a series of slightly curved parallel rows (Fig. 24*a, b*).

I happened to observe one of the mollusks in the act of laying eggs. The ribbon passed anteriorly, from the genital pore in the dorsal

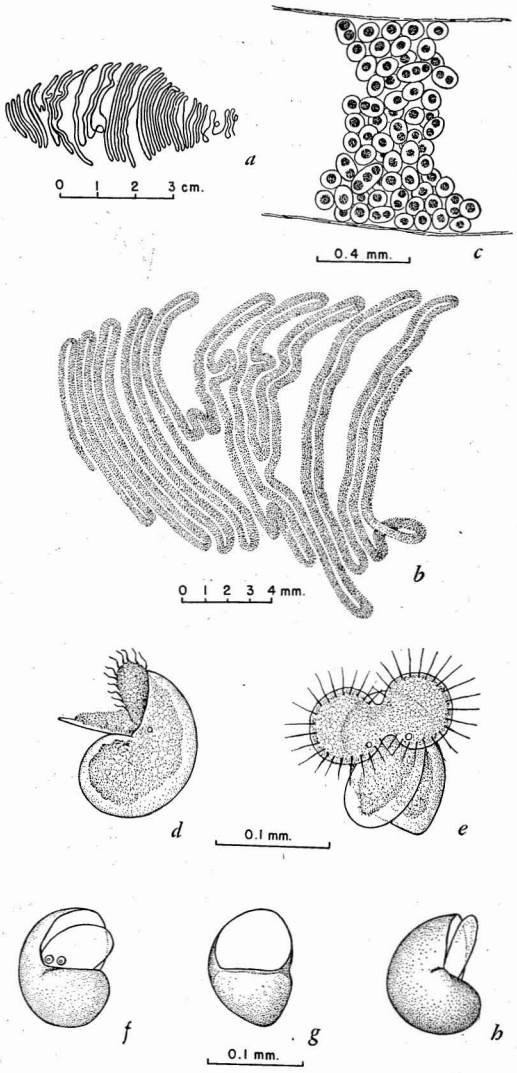

FIG. 24. *Dolabrifera olivacea* Pease. *a,* Egg ribbon; *b,* portion of egg ribbon enlarged; *c,* section of egg ribbon magnified to show arrangement of ova in egg envelopes; *d, e,* free-swimming veliger, lateral *(d)* and ventral *(e)* aspects; *f–h,* shell of free-swimming veliger showing operculum and otoliths.

slit, along the genital groove to the right side of the buccal disk. The mollusk then slowly moved its head from side to side, gradually backing up and carefully avoiding any overlapping of the ribbon.

As the embryos developed, the egg structures assumed a brownish or greenish color. Under magnification the egg ribbon was found to be closely packed with hyaline capsules, globular, oval, and a few oblong in form, each containing from one to three ova, usually one (Fig. 24*c*). The ova were about 0.08 mm. in diameter.

The free-swimming veliger stage was reached in 9 days. Larva and shell bore a close resemblance to those of *Tethys.* There was a well-developed, broad operculum extending well beyond the foot. No eyes were present but otocysts were. The larva had a faint yellowish or brownish tinge, while the shell was pale yellowish or golden. The length of the veliger shell was about 0.125 mm. (Fig. 24*d–h*).

Genus NOTARCHUS

Notarchus striatus Quoy and Gaimard
Fig. 25

An egg filament of *Notarchus striatus* was deposited in the laboratory, April 2, 1922. This egg structure, which was light brownish-yellow, was about 10 cm. in length, with a diameter of about 0.7 mm., and thrown into many irregular loops. A break in its length occurred in one place, as if the filament consisted of two parts (Fig. 25*a*).

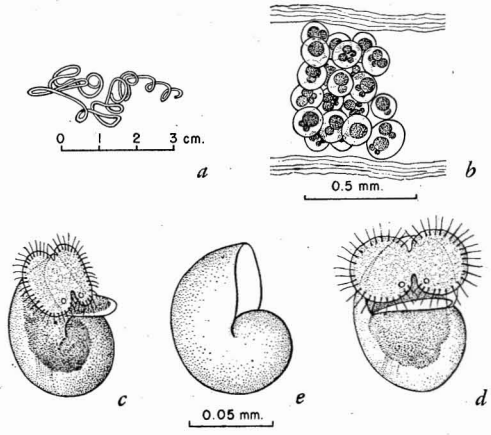

FIG. 25. *Notarchus striatus* Quoy and Gaimard. *a,* Egg filament; *b,* magnified section of filament with early cleavage stages; *c, d,* free-swimming veliger larva; *e,* shell of free-swimming veliger.

The parchment-like walls of the filament were rather thick and the lumen was tightly packed with ova. The ova, as in other genera of this family, were enclosed in hyaline capsules which usually contained one ovum. Sometimes there were two ova in a capsule, in which case the capsule was of an oblong form, instead of being globular or oval as were those containing only one ovum.

The diameter of the zygote was about 0.07 mm. and its first cleavage was unequal, as in *Tethys grandis,* resulting in one macromere and one micromere. The micromere divided next, equally, then the macromere, also equally, resulting in a stage of two macromeres and two micromeres. The two macromeres remained undivided, while the micromeres rapidly increased in number and formed a cap at the animal pole over the two yolk-laden macromeres at the vegetal pole (Fig. 25*b*).

The free-swimming veliger stage was reached in the short period of 6 days, when the handsome little larvae, whose shells measured but 0.09 mm. in length, emerged from the filament. The parts of the larva enclosed by the shell appeared to be straw colored, while the velum and foot were colorless; the veliger lobes were rather small and rounded, the operculum was broad and rounded and extended well beyond the foot. Otocysts were present, but no eyes. The columellar region of the shell had a light carmine tinge and the suture was of a deep reddish-brown. The rest was pellucid and colorless (Fig. 25*c, d, e*).

Family *HYDATINIDAE*

Genus HYDATINA

Hydatina amplustre (Linnaeus)

Fig. 26

On the morning of January 4, 1921, I found an egg receptacle in a glass dish with a *Hydatina amplustre*; this also served to identify several such structures that had been found close to the laboratory. The receptacle was a broad, white ribbon, intensely folded and attached to the surface of the dish with a broad adhesion disk. The ribbon had a width of about 1 centimeter and contained within its walls masses of ova enclosed in hyaline capsules. Development of the embryo was not investigated.

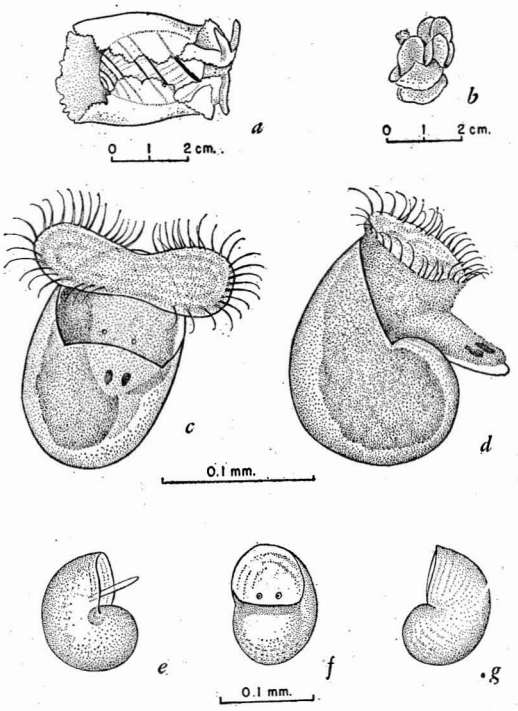

FIG. 26. *Hydatina amplustre* (Linnaeus). *a,* Animal that laid the egg structure; *b,* egg structure; *c, d,* free-swimming veliger: *c,* ventral, *d,* lateral aspects; *e–g,* shell of free-swimming veliger showing operculum and otoliths.

The free-swimming veliger possessed otocysts but not eyes. Two conspicuous elongate dark spots appeared on the ventral side of the foot near the tip, and an operculum was present on the opposite side. The clear, colorless veliger shell measured about 0.125 mm. in length (Fig. 26*a–g*).

Hydatina physis (Linnaeus)

Fig. 27

On November 16, 1922, an egg structure

attached to alga and later identified as that of *Hydatina physis* was found near the aquarium tank. It was about 25 mm. in length, half as wide, and intensely folded, much like that of *H. amplustre.* A single layer of hyaline capsules, each containing five or six embryos, lay between the walls of the structure (Fig. 27*a, b*).

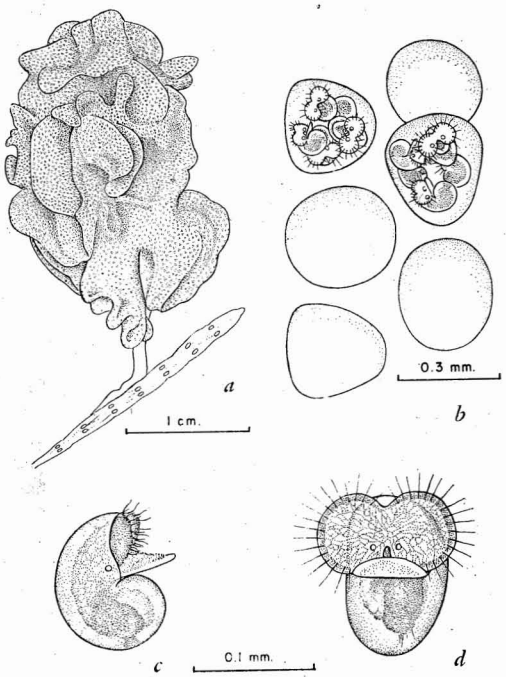

FIG. 27. *Hydatina physis* (Linnaeus). *a,* Egg structure; *b,* egg envelopes with veligers magnified; *c, d,* free-swimming veliger larva: *c,* lateral, and *d,* ventral aspects.

When the structure was obtained the embryos were far along in development. The veliger larva had a faint greenish tinge, and was a little smaller than that of *H. amplustre.* Otocysts and a prominent operculum were present. The shell, measuring 0.11 mm. in length, was colorless, like that of the preceding species. The muscle attaching the larva to the shell was clearly seen (Fig. 27*c, d*).

Family *ACTAEONIDAE*

Genus BULLINA

Bullina scabra solida Pilsbry

Fig. 28

A specimen of *Bullina scabra solida* found at Kahala reef was placed in a dish of water in the laboratory. Two days later, on the morning of March 23, 1921, the mollusk had deposited an egg filament in the dish.

The filament was a short, white, cylindrical tube, arranged in a spiral with one end attached to the bottom of the dish by means of a gelatinous material. The eggs were of varying sizes, quite numerous, and had no orderly arrangement within the structure, each being enclosed within a capsule. The animal was pure white and resembled closely *Hydatina amplustre* (Linnaeus) (Fig. 28*a, b, c*). Development was not observed.

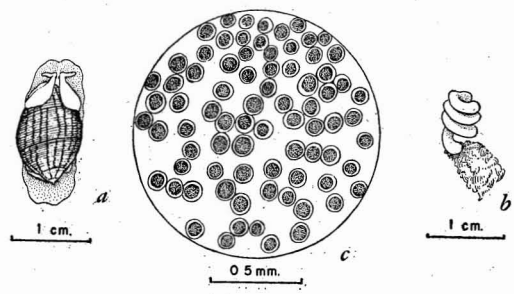

FIG. 28. *Bullina scabra solida* Pilsbry. *a,* Animal that laid the egg mass; *b,* egg filament; *c,* section of coil magnified.

Family *BULLIDAE*

Genus BULLA

Bulla sp.

Fig. 29

On November 22, 1922, two specimens of *Bulla* were brought to the laboratory from the adjacent water. An egg filament was laid by each mollusk the same day. These were comparatively thick cylindrical filaments, 3 cm. in length and 1 mm. in diameter. Each

contained a continuous string of ova wound transversely in circular loops. It could not be determined how the ova adhered to one another in a string. It seemed as if they were enclosed in an invisible gelatinous tube. Each ovum was enclosed in an oval capsule and had a diameter of about 0.06 mm. (Fig. 29*a, b*).

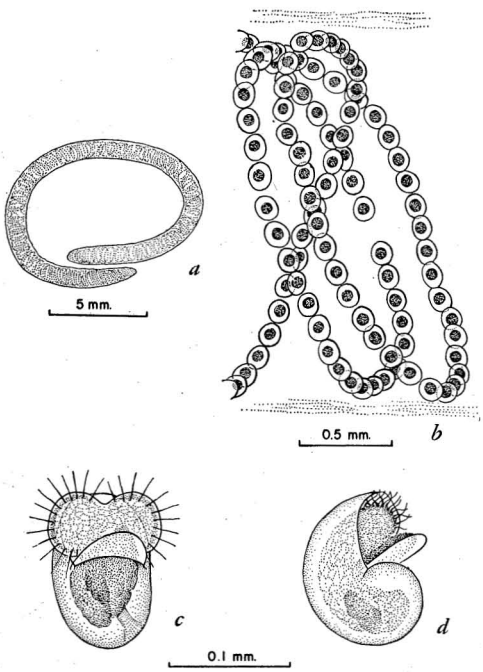

FIG. 29. *Bulla* sp. *a,* Egg filament; *b,* section of filament magnified to show arrangement of ova; *c, d,* free-swimming veliger larva: *c,* ventral, and *d,* partly lateral aspects.

The development of the zygotes was exceedingly rapid, the free-swimming veliger stage being attained in 4 days. The larvae and shells were colorless and neither eyes nor otocysts were present (Fig. 29*c, d*).

Family *AKERIDAE*

Genus HAMINOEA

Haminoea crocata Pease

Fig. 30

On March 27, 1923, several specimens of *Haminoea crocata* were brought to the laboratory from Waianae beach. Several egg filaments were laid by these animals. These filaments resembled those of the *Bulla* in their external characters as well as in the arrangement of the ova. The wall of the filament was thicker than in that of *Bulla* and each ovum was enclosed in a spherical capsule, instead of one of oval form as in *Bulla.* The diameter of the ovum was about 0.08 mm. The filament was about 4 cm. in length and about 5 mm. in diameter (Fig. 30*a, b*).

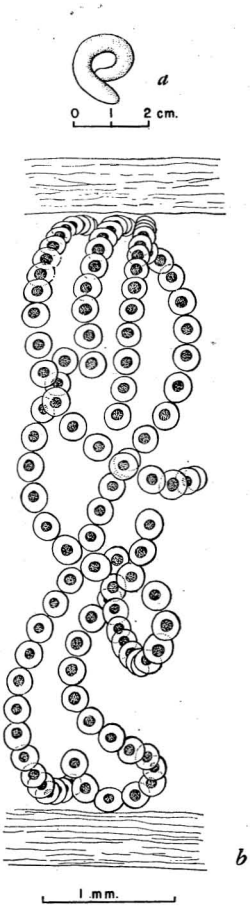

FIG. 30. *Haminoea crocata* Pease. *a,* Egg filament; *b,* section of filament magnified to show arrangement of ova.

Family *SCAPHANDRIDAE*

Genus ATYS

Atys semistriatus Pease

Fig. 31

On August 22, 1921, an egg mass was laid in the laboratory by a specimen of *Atys semistriatus* which had been found near-by.

The egg structure consisted of a globular mass of a soft, clear, gelatinous matrix, about 18 mm. in diameter, in which a thousand or more purple ova were imbedded in a spherical mass and surrounded by a thin layer of the matrix. Each ovum was enclosed in an oval hyaline capsule whose greatest diameter was about 0.2 mm.; the ovum measured about 0.09 mm. (Fig. 31*a, b*).

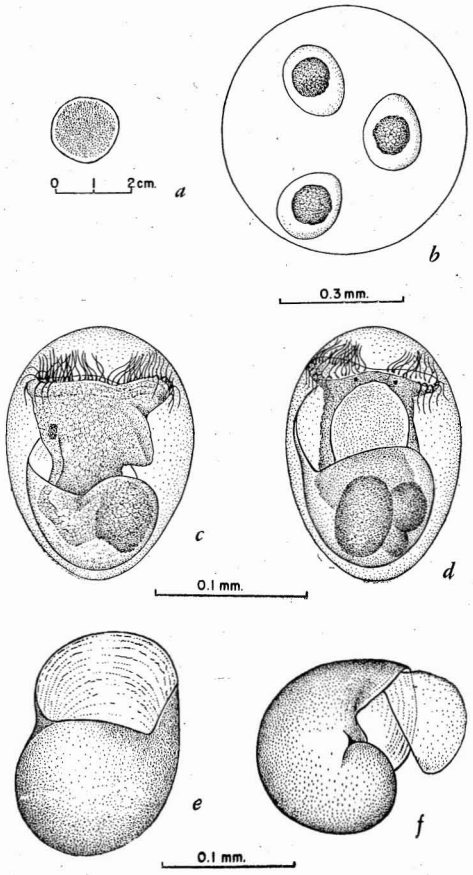

FIG. 31. *Atys semistriata* Pease. *a,* Egg mass; *b,* ova within hyaline capsules, magnified; *c, d,* veliger stage before hatching; *e, f,* shell of veliger larva with operculum.

Segmentation seemed very rapid, for the eggs, laid in the morning, were found to have attained a many-celled stage in the afternoon. Three macromeres were present at the vegetal pole, and the animal pole was capped with micromeres. About 24 hours later the embryos had become whirling ciliated gastrulas or trochophores.

The embryos did not reach their free-swimming stage, all dying within the matrix, but they reached an advanced veliger stage after 4 days' incubation. The velum was large with long cilia, the foot rather short and broad with a broad, triangular operculum. A rather ample, colorless, and transparent shell enclosed the visceral portion of the larva. A large purplish-red digestive gland could be seen in the region of the stomach, near which a well-defined intestine ran out to the anus beyond the margin of the shell. The eyes consisted of small pigment specks. Otocysts were not seen (Fig. 31*c–f*).

Family *UMBRACULIDAE*

Genus UMBRACULUM

Umbraculum sinicum (Gmelin)

Fig. 32

A specimen of *Umbraculum sinicum,* found near Waialua, Oahu, was brought to the laboratory. On the morning of June 25, 1921, a pink, garland-like egg structure was seen projecting from under its foot.

This structure consisted of a thin ribbon, 15 mm. in width, intensely folded upon itself and attached to the rock by one edge. It was wound three and one-half times around and measured about 12 cm. in diameter (Fig. 32*a*).

The ribbon was closely packed with globular capsules forming one or two layers. These capsules were quite uniform in size, 0.5 mm. in diameter, and each contained about 30 ova. A conservative estimate of the

number of ova contained in the whole structure gave the figure of 10,206,000 (Fig. 32*b*).

When examined in the morning of the day on which they were found the ova showed no signs of segmentation, but in the afternoon two- and four-cell stages were seen in many capsules, although many of the ova were still unsegmented. Adjoining capsules showed different stages of development, but the embryos in each capsule were usually of the same stage. The ovum was about 0.08 mm. in diameter and the first and second divisions resulted in blastomeres of nearly equal sizes (Fig. 32*c, d, e*). Succeeding stages of cleavage were not observed, but after the third day of incubation when the embryos had developed minute cilia, movement could be noticed. At the fourth day they showed high activity and the shell was apparently in the process of formation. A large, very conspicuous brown spot had now developed, usually on the right side of the body. After the sixth day of incubation the veliger lobes grew out and the shell covered the body. Neither eyes nor otocysts could be distinguished at this stage.

On the tenth day of incubation a large number of embryos launched upon their free-swimming larval existence. Otocysts, but no eyes, were present, as was a large operculum projecting beyond the tip of the foot and curving upward laterally. The shell was plain, colorless, and translucent (Fig. 32*f, g*).

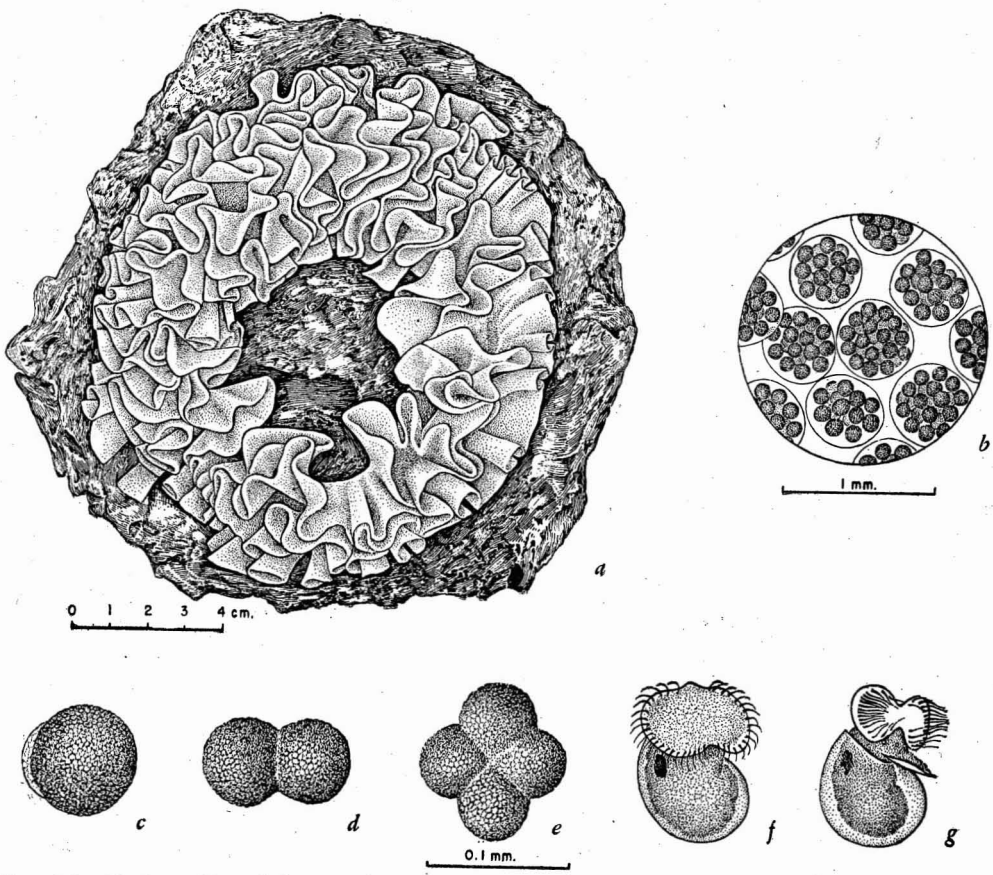

FIG. 32. *Umbraculum sinicum* (Gmelin). *a*, Egg ribbon; *b*, magnified section showing hyaline capsules with ova; *c–e*, cleavage stages; *f*, early veliger; *g*, free-swimming veliger larva.

Family *PLEUROBRANCHIDAE*

Genus PLEUROBRANCHUS

Pleurobranchus sp.

Fig. 33

On July 25, 1922, a small species of *Pleurobranchus* was found on the windward side of Moku O Loe, Kaneohe Bay, and brought to the laboratory. An egg filament, which for the size of the animal seemed very large, was laid by this mollusk. It was about 18 cm. in length with a diameter of about 4 mm. It was white and transparent and contained what appeared to be a continuous thick-walled tube wound circularly with the filaments in close contact with one another. A single layer of ova, each ovum measuring about 0.08 mm. in diameter and enclosed by a spherical capsule, lay closely packed within this inner tube (Fig. 33*a, b*).

The embryos attained their free-swimming larval stage in 6 days, at which time they had a pair of large, rounded, colorless veliger lobes with conspicuous eye spots, a pointed foot without a visible operculum, otocysts, and a large black pigment spot located near the left side. The viscera were pale greenish-yellow. The shell, which measured 0.125 mm. in length, was clear and colorless (Fig. 33*c–g*).

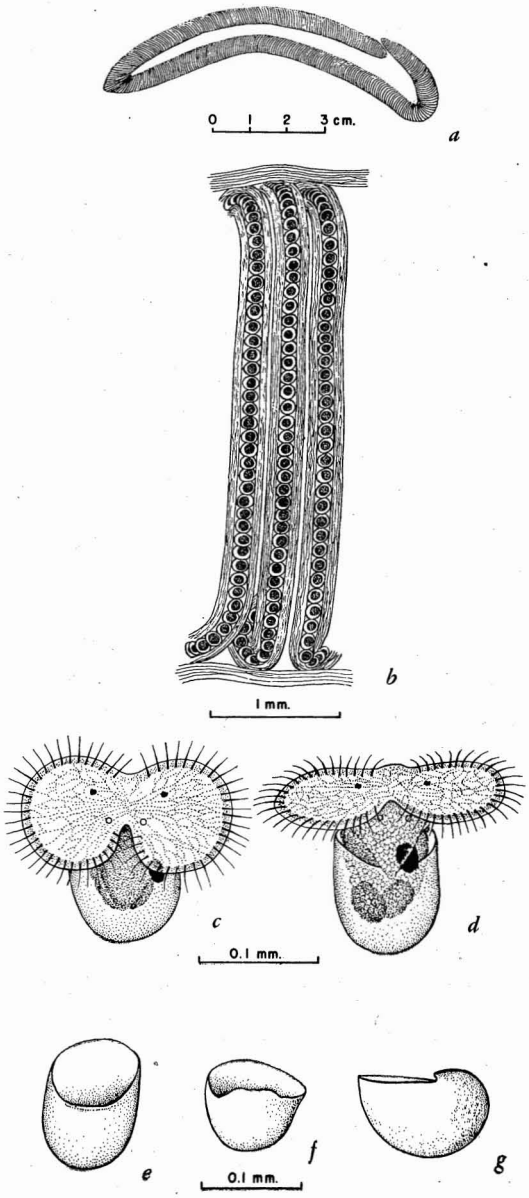

FIG. 33. *Pleurobranchus* sp. *a,* Egg filament; *b,* magnified section of filament showing circularly arranged tubes containing ova; *c, d,* free-swimming veligers; *e–g,* shells of free-swimming veligers.

Suborder ASCOGLOSSA

Family *PLACOBRANCHIDAE*

Genus PLACOBRANCHUS

Placobranchus sp.

Fig. 34

A large number of *Placobranchus* sp. was brought in from Molokai in late February, 1923, and kept in the living state in the laboratory for several months. None of these laid eggs. But a specimen found near the Elk's Club, Waikiki, during March, 1923, deposited a white cylindrical filament, about 19 mm. in length and nearly 1.5 mm. in diameter, which tapered to a point at each end. At the middle of the filament, the ova lay 9 or 10 abreast in cross section; each was enclosed in a globular capsule of about 0.16 mm. in diameter (Fig. 34*a, b*).

The first two cleavages resulted in blastomeres of equal sizes as in the typical gastropod. The embryo reached the free-swimming larval stage in 8 days. Larva and shell were clear and transparent, the operculum large and rounded. Otocysts were present but not eyes. The veliger shell measured 0.14 mm. in length (Fig. 34*c, d*).

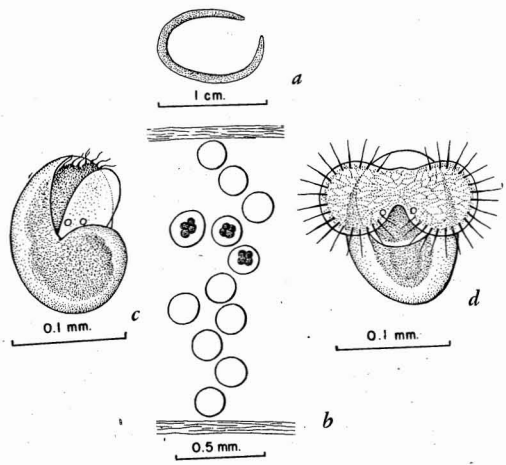

FIG. 34. *Placobranchus* sp. *a,* Egg filament; *b,* magnified section of filament showing 4-cell cleavage stage; *c, d,* free-swimming veliger larva.

Family *ELYSIIDAE*

Genus ELYSIA

Elysia sp.

Fig. 35

Several animals of this genus were found near the laboratory close to shore. An egg filament was deposited in the laboratory by one of them on July 5, 1923. This was a white, cylindrical, twisted filament about 25 mm. in length, closely packed with egg capsules of oval and angular shapes, each containing from two to four ova. The diameter of the ova was about 0.08 mm. (Fig. 35*a, b*).

The free-swimming veliger stage was reached in the short period of 5 days, when the colorless larvae in a pellucid and colorless shell emerged from the coil. The operculum extended beyond the foot; otocysts were present but not eyes (Fig. 35*c*).

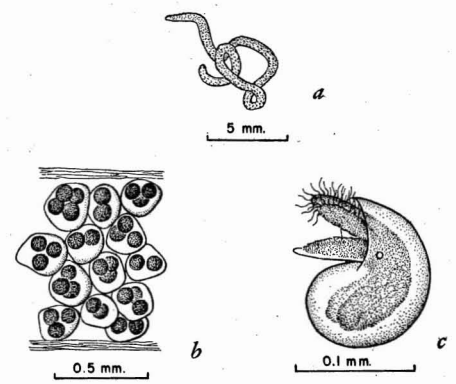

FIG. 35. *Elysia* sp. *a,* Egg filament; *b,* magnified section of filament showing arrangement of ova and hyaline capsules; *c,* free-swimming veliger larva in lateral aspect.

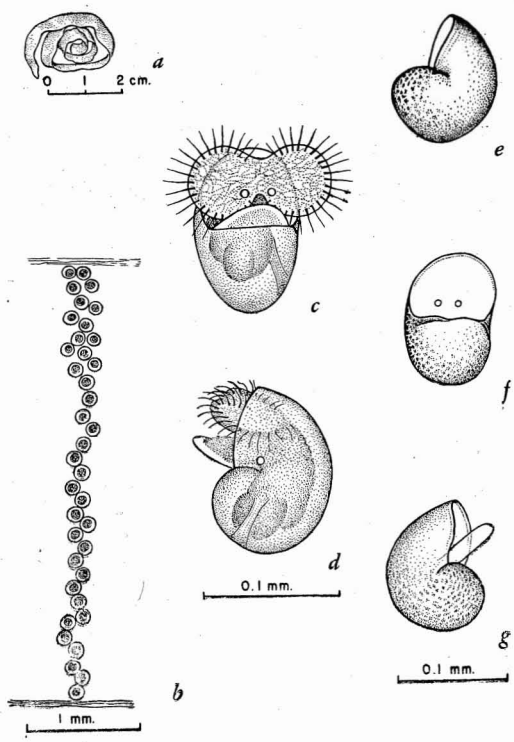

FIG. 36. *Cryptodoris* sp. *a,* Egg ribbon; *b,* magnified section of ribbon showing arrangement of ova; *c, d,* free-swimming veliger larva: *c,* ventral, and *d,* lateral aspects; *e–g,* shell of free-swimming veliger larva with operculum and otocysts.

Suborder NUDIBRANCHIATA
Family *DORIDIDAE*

Genus CRYPTODORIS

Cryptodoris sp.
Fig. 36

During the night of December 10, 1922, an egg ribbon was deposited in the laboratory by an animal of the genus *Cryptodoris.* This was a bright yellow ribbon of three volutions. It was about 4 mm. in width and filled with globular egg capsules, each containing an ovum. There were about 30 ova abreast in cross section. The ova were about 0.06 mm. in diameter (Fig. 36*a, b*).

As the embryos developed, the ribbon turned bright copper color and the free-swimming veliger stage was attained in about 10 days. The shell at this stage was about 0.12 mm. in length and of a bright copper color on the apical side of the columella. The veliger lobes were round with long cilia and the operculum prominent. No eyes were present but otocysts were. A larval muscle was clearly seen (Fig. 36*c–g*).

Genus GLOSSODORIS

Glossodoris sp.
Fig. 37

In March, 1923, two animals of this genus were brought to the laboratory from Waianae. An egg ribbon was deposited by one of them during the night of March 17, 1923. This consisted of a flat white band about 4 mm. in length and of one volution. About 10 ova were seen abreast in cross section, each enclosed in a spherical capsule about 0.14 mm. in diameter (Fig. 37*a, b*).

Family *HEXABRANCHIDAE*

Genus HEXABRANCHUS

Hexabranchus sp.
Fig. 38

On May 21, 1923, an egg structure was deposited in the laboratory by this beautiful nudibranch, several specimens of which had been kept living for months in aquarium jars.

A few days after the first egg structure was found, a second and larger one with one volution more than the first was deposited by the mollusk. A study was made of the first structure. This was a bright scarlet to orange,

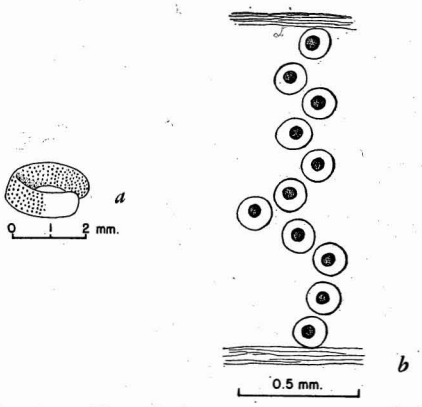

FIG. 37. *Glossodoris* sp. *a,* Egg ribbon; *b,* magnified section of ribbon showing arrangement of ova.

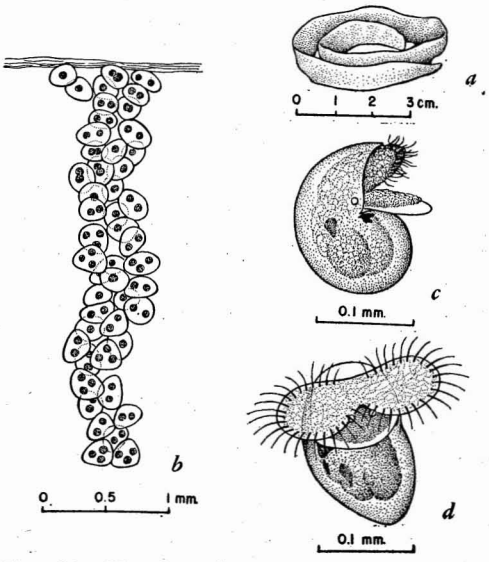

FIG. 38. *Hexabranchus* sp. *a,* Egg ribbon; *b,* magnified section of ribbon showing arrangement of hyaline capsules and ova; *c, d,* free-swimming veliger larva: *c,* lateral, and *d,* ventral aspects.

flat ribbon of two volutions, about 14 cm. in length and 6 mm. in width. The structure was closely packed with oval and triangular egg cases containing from one to three ova each. The ova were about 0.06 mm. in diameter (Fig. 38*a, b*).

The free-swimming stage was attained in 9 days, when a pale brownish larva emerged. On the right side of the body of the larva was an irregular black pigment spot and near it another of dark orange. Otocysts were present, but not eyes. A broad operculum and a clear and pellucid shell were present (Fig. 38*c, d*).

Family *AEOLIDIIDAE*

Genus AEOLIDIA

Aeolidia sp.

Fig. 39

During the month of April, 1922, a number of egg structures were deposited on a rock in the laboratory by a species of *Aeolidia.* They were flat, bright yellow ribbons about 18 mm. long and 2 mm. wide, of one volutions which was so close that the inner margins, by which the mass was attached, almost touched (Fig. 39*a, b*). The ova were strung out in single rows within transverse gelatinous tubes which radiated from the inner margin of the ribbon. A row contained an average of 15 ova. The spaces between the transverse tubes toward the outer margin also contained ova (Fig. 39*c*). The ova, which measured about 0.17 mm. in diameter, were contained singly in oval capsules.

This is the most prolific mollusk in point of numbers of egg structures yet observed. Nine ribbons were deposited by the same animal within 12 days, one each day for several days. Two more mollusks of this species were brought in from near the Elk's Club, Waikiki. Both animals were on a living coral head, *Porites compressa,* to which were attached half a dozen or more egg ribbons. During 10 days of captivity the number of ribbons deposited by them had increased to 30. The ribbons were all of a very pale yellow and nearly all of them were larger than those of the first lot, most of them being twice as great in diameter.

The eggs of all the ribbons seemed to develop and the free-swimming stage was reached in 6 days. The eyespots in this larva were large and prominent, as were foot and operculum. The viscera had a marked yellowish tinge, but the foot and velum were almost colorless. The shell, measuring 0.225 mm. in length, is pellucid and colorless (Fig. 39*e, f*).

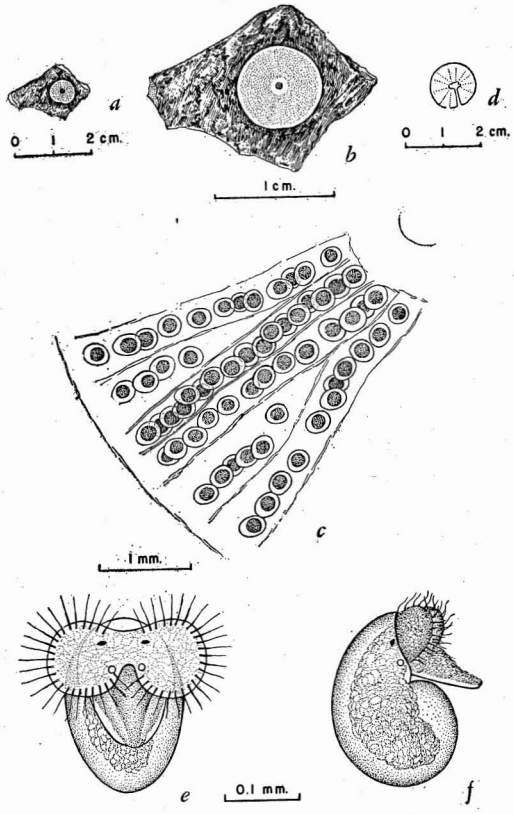

FIG. 39. *Aeolidia* sp. *a,* Egg ribbon; *b,* ribbon enlarged; *c,* magnified section of ribbon showing arrangement of ova; *d,* egg ribbon laid by another individual; *e, f,* free-swimming veliger larva: *e,* ventral, and *f,* lateral aspects.

Family *FIMBRIIDAE*

Genus MELIBE

Melibe pilosa Pease

Fig. 40

Early in February, 1922, some egg structures were deposited in the laboratory by specimens of *Melibe pilosa* found close to the laboratory pier. The egg structure consisted of a very thin, broad, white ribbon, greatly folded, and spirally wound several turns, united by the inner edges, by which it was attached to a rock or other object (Fig. 40*a*). Transversely arranged within the capsular wall, and closely filling the space, was a cylindrical tube packed with egg cases arranged in a single row. These egg cases, or hyaline envelopes, had the shape of a hen's egg and measured about 0.17 mm. by 0.25 mm. Each case contained one ovum which had an average diameter of 0.125 mm. (Fig. 40*b*).

Development of the embryo was not investigated, but a study of the veliger shell was made. This was elongate, pellucid and colorless, about 0.2 mm. in length (Fig. 40*c, d*).

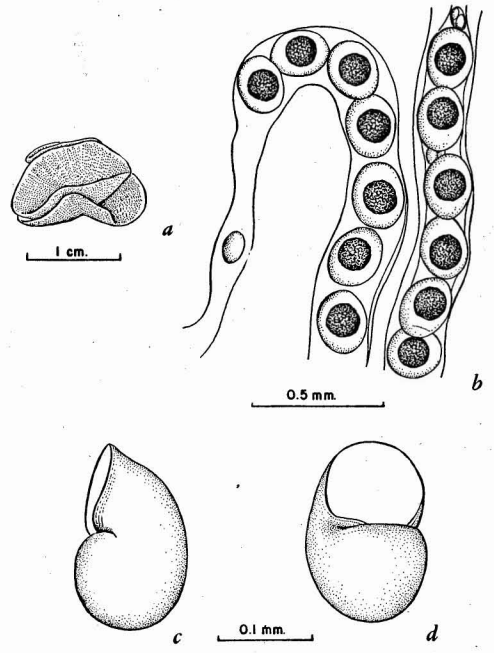

FIG. 40. *Melibe pilosa* Pease. *a,* Egg ribbon; *b,* magnified section of ribbon showing ova in hyaline capsules contained in tubes; *c, d,* shell of free-swimming veliger.

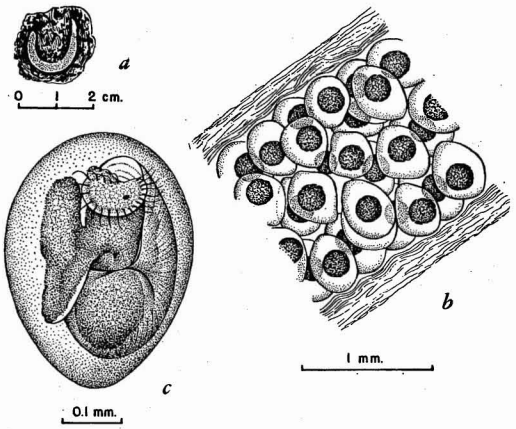

FIG. 41. *Siphonaria normalis omara* Reeve. *a,* Egg ribbon; *b,* magnified section of ribbon showing compact masses of hyaline capsules with ova; *c,* unhatched veliger stage.

Order PULMONATA

Family *SIPHONARIIDAE*

Genus SIPHONARIA

Siphonaria normalis omara Reeve

Fig. 41

On September 9, 1923, a specimen of *Siphonaria* deposited an egg structure in the laboratory, several of the animals having been brought in from the near-by sea wall. The egg structure was a somewhat thickened colorless ribbon, arranged in a half circle which measured about 3 cm. in length and 2 mm. in width. The walls of the ribbon were very thick and fibrous, and the eggs were closely packed in two layers. A rather ovoid hyaline envelope surrounded each ovum. This envelope measured about 0.485 mm. in length and 0.34 mm. in width; the diameter of the ova was about 0.19 mm. (Fig. 41*a, b*).

Steps in development were not observed, but a study of the embryo when it had reached the veliger stage was made. The color of the animal was pale greenish, while that of the

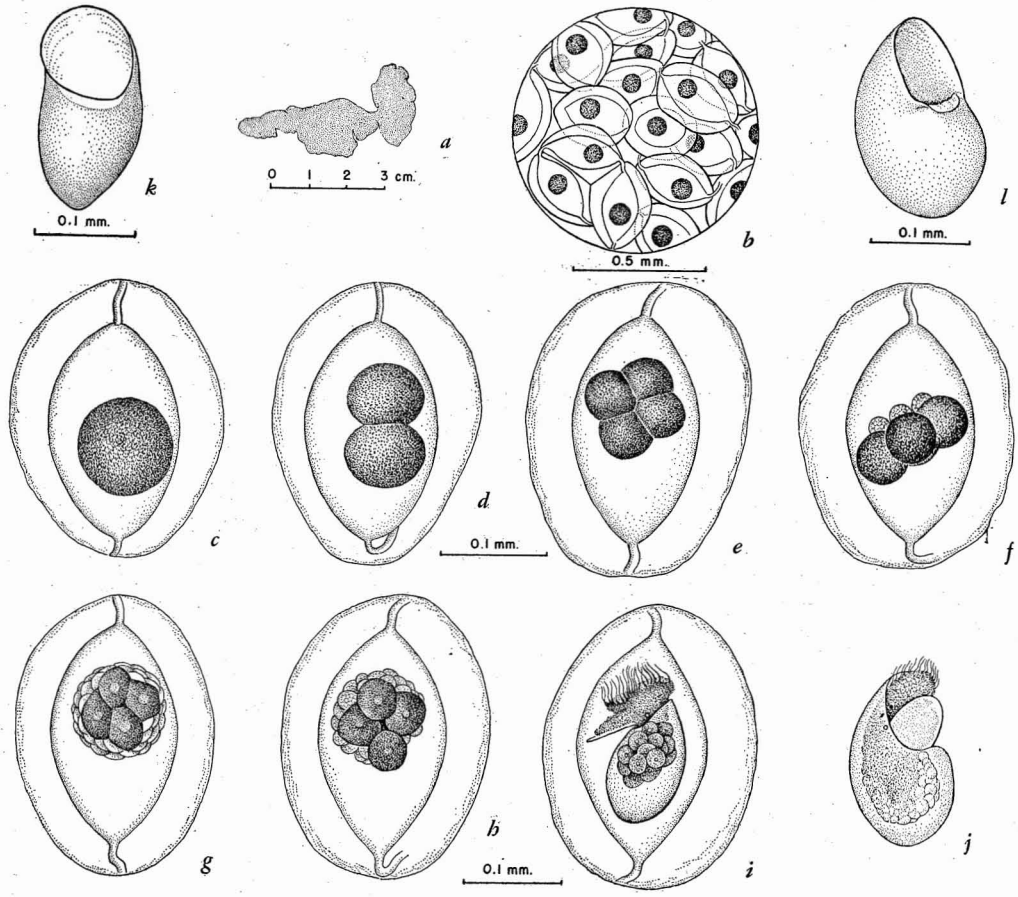

FIG. 42. *Peronia* sp. *a,* Egg structure; *b,* magnified section of egg structure showing a double capsular enclosure for ova; *c–g,* cleavage stages; *h,* gastrula ?; *i,* early veliger with extremely large endodermal cells; *j,* free-swimming veliger; *k, l,* shell of free-swimming veliger.

shell was brown. Eyes were present. The foot was large with a conspicuous operculum. The shell was about 0.33 mm. in length (Fig. 41*c*). The embryos all died, so the free-swimming stage was not observed.

Family *ONCHIDIIDAE*

Genus PERONIA

Peronia sp.

Fig. 42

Early in September, 1921, a number of specimens of *Peronia* were gathered from crevices in the sea wall near the laboratory. These were placed in a jar with running water, from which they soon escaped, being air-breathers, and scattered all over the aquarium tables. Some crawled into dark, wet corners of wooden boxes, where they seemed to thrive. Some lived thus for months in the laboratory. It is obvious that this mollusk cannot live under water, while, on the other hand, it needs to be kept wet constantly with sea water. It has been found at Kaena Point and Black Point on the shore rocks above high tide level and where only the spray could reach it. A large number of these mollusks were found at Kawailoa, Oahu, during June.

Eggs were deposited in the laboratory by one of these animals on September 3, 1921. Since that time they have often been obtained from other individuals. The egg structure was a lemon-yellow, tough, gelatinous mass with irregular outlines, pasted flatly onto any surface. The ova were closely packed throughout the whole structure and each was enclosed within a double capsule. The diameter of the ovum was about 0.08 mm. The lesser diameter of the inner capsule, which was of a regular oval or oblong form, was 0.14 mm., its greater diameter being 0.22 mm. The lesser diameter of the outer capsule, which was of an irregular oval or somewhat baggy shape, was 0.2 mm.; its greater diameter was about 0.28 mm.

The relations of the capsules to one another appeared to be as follows: from each end of the inner capsule sprang a slender tube or thread which united with another inner capsule, penetrating the outer capsule in doing so, forming thus a continuous, closely united string of egg capsules thrown promiscuously together (Fig. 42*a, b*).

Cleavage of the zygotes commenced the same day they were laid, the 4-cell stage being reached during the afternoon. The first two divisions were equal and the third resulted in four micromeres at the animal pole of the macromeres; hence it was typical of gastropod cleavage (Fig. 42*c–f*).

A many-celled, or morula, stage was reached after 24 hours. The four undivided macromeres showed up distinctly at the vegetal pole, their nuclei appearing as clear globules. From the animal pole numerous micromeres extended beyond the equator. Soon a contraction of each of the four undivided macromeres took place, rounding off their former angular outlines and leaving an opening between them (the gastropore?) at the vegetal pole. Cleavage of the macromeres seemed greatly retarded, probably due to the obstruction of the yolk. This is typical epibolic gastrulation (Fig. 42*g, h*).

The extremely slow division of the macromeres, or endodermal cells, remained a characteristic feature of the development of this mollusk. Even when the veliger stage was reached, these cells appeared as a large cluster, each with a distinct, rounded outline and a clear central nucleus (Fig. 42*i*).

The free-swimming stage was attained after 9 days of incubation, when a veliger larva appeared within an elongate, clear, colorless shell which was nearly bilaterally symmetrical. The foot bore a broad, anteriorly rounded operculum. Eyes, as well as otocysts, were present. The endodermal cells, still large and conspicuous, were of a bright yellow or brassy color (Fig. 42*j, k, l*).

CONCLUSIONS

Pelagic Stage and Distribution

Of all the species studied—those included in this paper and others to be reported upon later—41 attained the veliger stage. Of these, 40 were found to have a pelagic stage, thus giving the high figure of 97.5 per cent pelagic or free-swimming larvae.

This seems remarkable in view of the fact that Thorson (1940) reports 75 per cent from the Iranian Gulf as the highest percentage in a list prepared by him, while next highest he quotes Risbec from New Caledonia with 57 per cent. He shows a general increase in pelagic larvae from the colder to the warmer waters, beginning with none in East Greenland and ending with 75 per cent for the Iranian Gulf.

It appears that temperature is of much importance in determining the pelagic stage, but there seem to be other controlling factors also. When the isolation of the Hawaiian Islands caused by their vast ocean barriers is considered, it may be inferred that its molluscan population must have depended upon a pelagic or free-swimming stage of sufficient duration to enable the larvae to be carried by currents from islands in the Pacific support-

ing a gastropod fauna similar to the one of Hawaii. Such faunas are found in Micronesia. We may then postulate that ocean currents from that region were the source of distribution of the marine gastropods of Hawaii. The veliger larva could be carried east by the North Equatorial Current, which, along its course, might yield parts of its planktonic cargo to the westward-flowing Japan Current to be carried by it to the Hawaiian Archipelago. If this be the chief, or only, method of deriving our marine gastropod fauna, we must at once recognize the importance of a long free-swimming existence to the successful migration over vast ocean barriers.

Phylogenetic Significance of Veliger Shell

The great dissimilarity between the veliger larva and the adult gastropod may have its explanation on the basis of adaptation on the one hand and heredity on the other. To structures that have developed as adaptive measures in the larva is applied the term cenogenetic in contradistinction to the term palingenetic, which deals with characters of ancestral significance, thus throwing light upon the evolutionary history of the organism.

The ciliated veliger lobes by means of which the larva leads its pelagic existence appear important to the distribution of numerous species and might therefore be classed as an adaptation. We can, however, conceive of a minute gastropod ancestor, which, like the wheel animalcule (Rotifera), was provided with ciliated lobes that served both for locomotion and food getting before it developed its protective shell. Concerning the veliger shell it will be noted that it was present in the opisthobranch larva as well as in that of the prosobranch, even in groups where it is entirely lacking in the adult animal. In addition to the veliger shell an operculum was found in all but two species, *Conus hebraeus* and *Pleurobranchus* sp. I have failed to see any service of the operculum to the veliger larva. During the active existence of the larva, the foot with its operculum was fully extended, and only when a larva sank to the bottom to die was the operculum seen to close the aperture to the shell.

Veliger larva and shell both show a close approach to a bilateral symmetry, which in later development is lost by coil formations. It appears that both the veliger larva and the shell with the operculum have a palingenetic significance in which the swimming apparatus, the veliger lobes, have been retained owing to their functional value, coming to overlap in time, as it were, a later ancestral structure, the shell.

Supportive evidence for such a contention may be found in a comparison of the veliger shell with some of the fossil gastropods of the early Paleozoic era, Cambrian and Ordovician, which show simple shells of bilateral symmetry and from which might be derived the divergent groups, viz., the coiled snail on the one hand and the naked slug on the other.

One may readily observe a similarity in the structure of spawn as well as in larval peculiarity in species of the same genus and more so, perhaps, if the species are closely related. Such a condition may then parallel to a large extent the taxonomic position assigned to the adult forms and, therefore, be of taxonomic value.

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